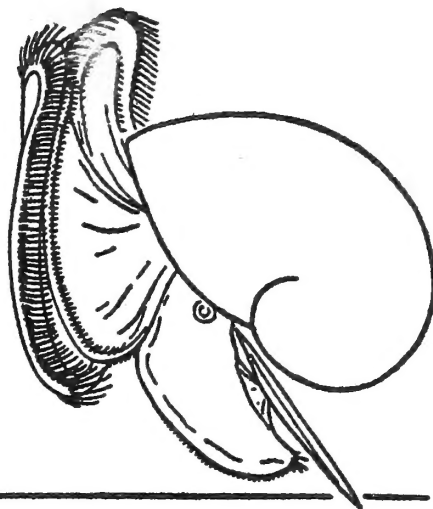


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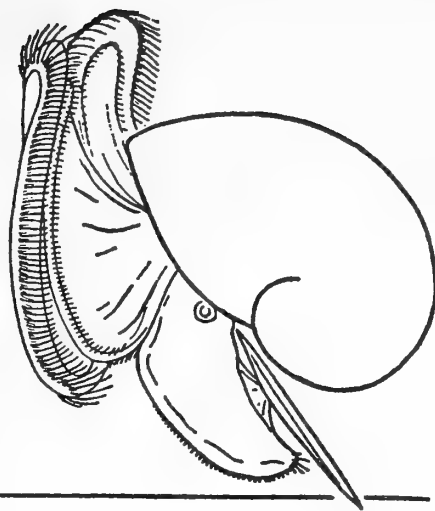


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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

Recent Eastern Pacific Species of the Crassatellid Bivalve Genus *Crassinella*

BY

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(4 Plates)

MARINE DREDGING IN SHALLOW water throughout the Panamic faunal province frequently reveals large quantities of small bivalves of the genus *Crassinella*. During an attempt to determine which, if any, members of this genus are living as far north as the West Coast of the United States, I found that the nomenclature of the northwest American species of the genus was much in need of review. The following is the product of an effort to fill that need.

Members of the genus *Crassinella* are veneroid bivalves, with true hinge teeth and eulamellibranch ctenidia. Like other members of the Crassatellacea, they have no more than 2 cardinal teeth in each valve and have long, thin lateral teeth. They are similar to other members of the Crassatellidae in having an internal ligament and in lacking an outer demibranch on their ctenidia (HARRY, 1966; ALLEN, 1968). *Crassinella* and certain other genera of this family are sometimes separated off as the subfamily Scambulinae, chiefly on the basis of their opisthogyrate or orthogyrate beaks. Other members of this subfamily are extinct (CHAVAN in COX *et al.*, 1969: N-577).

Many members of the genus *Crassinella* are opisthogyrate. In some species, the beaks are strongly twisted posteriorly. However, in others, the beaks are more or less orthogyrate. Whether or not the beaks are conspicuously opisthogyrate, these small clams often appear to be "backwards" for other reasons. Their lunule is narrow, whereas their escutcheon is wide and lunule-like. This has often confused workers, who have confounded left and right valves and gotten anterior and posterior mixed up in descriptions of hinge structures. The correct orientation is suggested by the position of the ligament (as in the majority of bivalves, posterior to most hinge elements) and confirmed by the arrangement of the soft parts (siphons, palps, foot, etc.) (see HARRY, 1966: fig. 1; ALLEN, 1968: fig. 2a).

HARRY (1966) discussed Recent members of the genus *Crassinella* in the northwestern Gulf of Mexico, providing an extensive commentary on *C. lunulata* (CONRAD, 1834: 133), as well as notes on the type species of the genus, *C. martinicensis* (Orbigny, 1846). ALLEN (1968) discussed the functional morphology of *C. mactracea* (LINSLEY, 1845: 275; 2 figs.), a probable synonym of *C. lunulata*. Previous listings of members of the genus are to be found in TRYON (1872), SMITH (1881), and LAMY (1917).

HARRY (1966) outlined the nomenclatural entanglements of the generic unit now called *Crassinella*. The various questions having been resolved, the results of the unraveling can be presented as follows:

Crassinella GUPPY, 1874: 442

Type species by M: "*C. martinicensis* d'Orb." =

Crassatella martinicensis ORBIGNY, 1846: 288-289; plt. 27, figs 21-23

= *Pseuderiphyla* FISCHER, 1887: 1022

(Type species by M: *C. martinicensis* Orbigny)

= *Crassatella*, *auctt.*, non LAMARCK, 1799: 85

= *Thetis*, *auctt.*, non C. B. ADAMS, 1845: 9 (a venerid bivalve), which itself was non J. SOWERBY, 1826: 19; plt. 513 (a mactromyid bivalve)

= *Gouldia*, *auctt.*, non C. B. ADAMS, 1847: 29 (a new name for *Thetis* C. B. ADAMS, 1845, non J. SOWERBY, 1826)

= *Eriphyla*, *auctt.*, non GABB, 1864: 180 (as *astartid* bivalve)

Important features in the classification of members of this genus are:

- (1) Shape – general outline
relative size of the anterior and posterior ends
shape of the posterior end
orientation of the beaks
- (2) Size

- (3) Surface sculpture – smooth, rounded ribs, lamellae
- (4) Hinge teeth – presence of uniquely shaped elements

One of the unique features of the shells of *Crassinella* is their unusual external texture. CARPENTER (1857b: 83) described this texture as resembling “strung figs.” HARRY (1966: 70, 73-74) described this texture in detail, terming it as being composed of “elongate, swollen polygonal units.” This pattern, which is here termed “cellular,” is of minor importance in distinguishing species from one another.

On the basis of the important features for classification given above, the eastern Pacific species may be keyed as follows:

KEY TO RECENT AND PLEISTOCENE WEST AMERICAN *Crassinella*

- 1. Anterior end shorter and sculpture of even, rounded ribs *C. skoglundae* (spec. nov., herein)
Beaks central, or closer to posterior end (rarely with shorter anterior end; if so, sculpture of irregular; lamellar ridges) 2
- 2. Beaks central to subcentral 3
Beaks closer to posterior end 6
- 3. Beaks pointed; posterior end angular, pointed, or produced; right valve without posterior cardinal; sculpture almost always present, lamellar 4
Beaks rounded; posterior end subangular to rounded; right valve with a posterior cardinal; sculpture, when present, of rounded ribs 5
- 4. Posterior end pointed but not rostrate; postero-dorsal margin straight to slightly concave; shell to 10 mm or more in length *C. pacifica*

Posterior end rostrate; postero-dorsal margin strongly concave; shell to only 4.6 mm in length

..... *C. ecuadoriana*

- 5. Shell nearly smooth, or with low concentric ribs concentrated near beaks *C. varians*
Shell with even, heavy concentric ribs *C. coxa*
- 6. Sculpture of even, rounded concentric ribs; interspaces narrow; left valve with a short, peg-like posterior cardinal *C. adamsi*
Sculpture concentrated near beaks, obsolete ventrally; interspaces as wide as ribs; left valve with an elongate, ventrally directed posterior cardinal
..... *C. nuculiformis*

In the present study, I made an attempt to locate the type material of each nominal west American taxon and to photograph the holotype or a potential lectotype of each. I also studied all the Recent material in the collections of the United States National Museum of Natural History, the California Academy of Sciences, the Los Angeles County Museum of Natural History, the American Museum of Natural History, and Stanford University (now in the California Academy of Sciences), as well as in the private collections of Mrs. Carol C. Skoglund and Mr. Bertram C. Draper.

Each species account contains a synonymy, with references listed in chronological order under each species name. Changes in generic assignment are given in brackets before the reference in which the change is first made. This is followed by information about the type material and type locality of each nominal taxon. Then I have included a detailed description of each species, and an account is given of their geographic distribution and habitat. For some species, an additional discussion is provided.

Explanation of Figures 1 to 6

Figure 1: *Crassinella pacifica* (C. B. Adams), lectotype (restricted herein), external and internal views (left valve); MCZ 186 297; Panama Bay, Panama; length, 4.9 mm

Figure 2: *Crassinella pacifica* (C. B. Adams). Holotype of *C. mexicana* Pilsbry & Lowe; external and internal views (left valve); ANSP 155622; Guaymas, Mexico; length, 3.4 mm

Figure 3: *Crassinella pacifica* (C. B. Adams). External view of right valve; CAS 59982; Panama Bay, Panama; length, 6.4 mm

Figure 4: *Crassinella pacifica* (C. B. Adams). External view of right valve and internal view of both valves; LACM 71-183; Bahía Magdalena, Baja California Sur; length, 7.3 mm

Figure 5: *Crassinella lunulata* (Conrad, 1834). Holotype of *C. oregonensis* Keen; external view (left valve); CAS-SUPTC 6052; Coos Bay, Oregon; length, 5.6 mm

Figure 6: *Crassinella ecuadoriana* Olsson, holotype, external and internal view of both valves; ANSP 218934; Puerto Callo, Ecuador; length, 2.9 mm

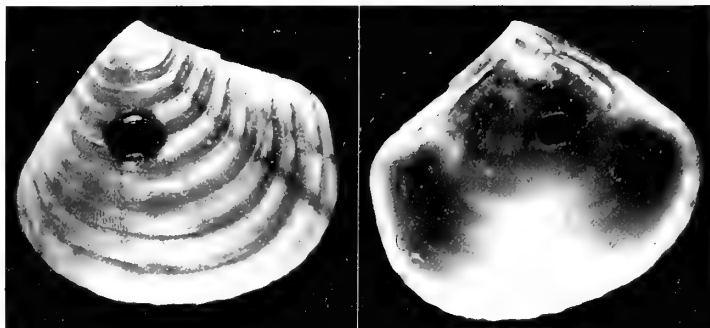


Figure 1

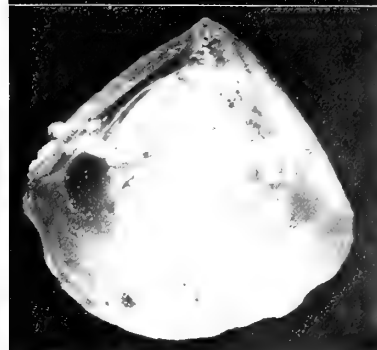
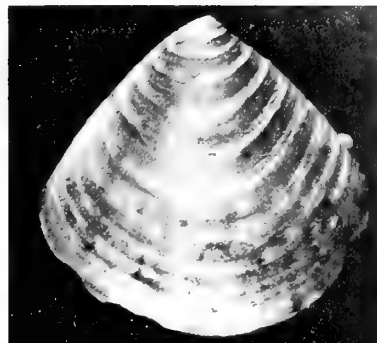


Figure 2

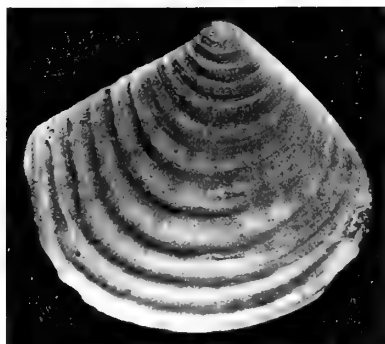


Figure 3

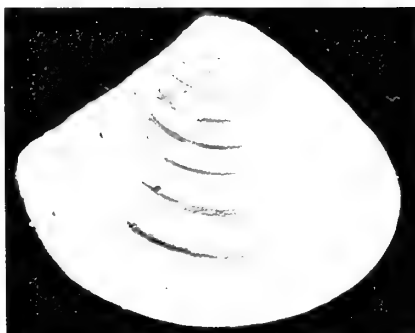


Figure 4

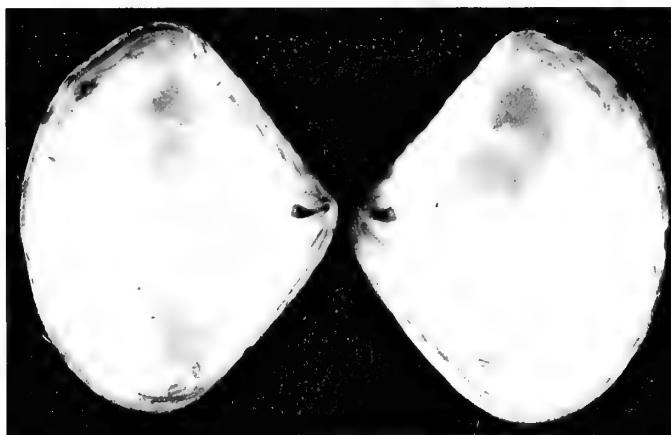


Figure 4

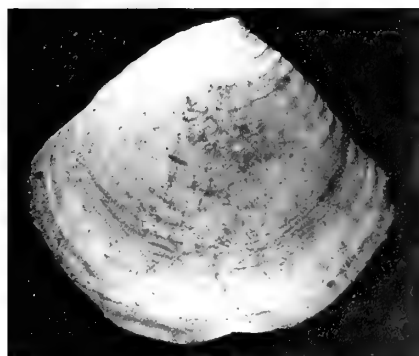


Figure 5

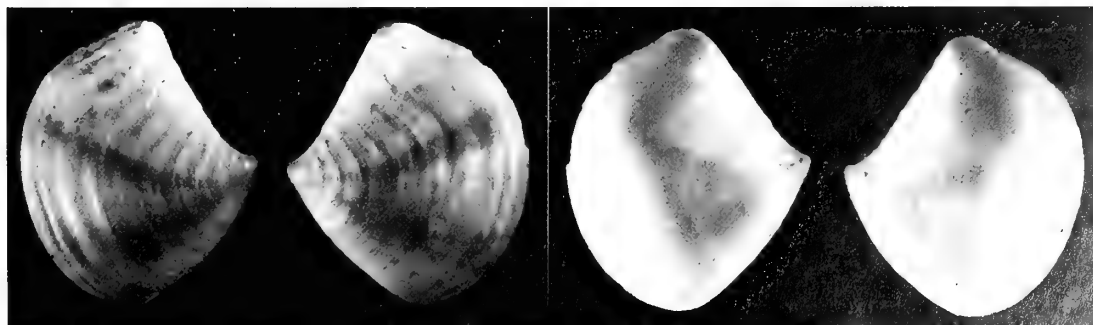


Figure 6

The following abbreviations are used in the text:

- ANSP — Academy of Natural Sciences of Philadelphia
 AHF — Allan Hancock Foundation [material partly in the LACM]
 BM(NH) — British Museum (Natural History)
 CAS — California Academy of Sciences [GTC — Geology Type Collection]
 LACM — Los Angeles County Museum of Natural History
 MCZ — Museum of Comparative Zoology, Harvard University
 SUPTC — Stanford University Paleontology Type Collection [now at CAS]
 USFC — United States Fish Commission (localities)
 USNM — United States National Museum of Natural History
 m — meter(s)
 km — kilometer(s)
 SD — standard deviation

Crassinella pacifica (C. B. Adams, 1852)

(Figures 1 to 4)

Gouldia pacifica C. B. Adams, 1852

- C. B. ADAMS, 1852a: 499, 545 [1852b: 275, 321]
 CARPENTER, 1857a: 247, 278, 306, 364
 CARPENTER, 1857b: 82-84, 86, 549
 CHENU, 1862: 130; fig. 620
 CARPENTER, 1864a: 365 [1872: 201 (= 27)]

[*Crassatella*]

- CARPENTER, 1864b: 544, 552 [1872: 30, 38]

[*Crassatella* (*Crassinella*)]

- LAMY, 1917: 248-249

[*Crassinella*]

- PILSBRY & OLSSON, 1941: 56

- BURCH, 1944: 9

- HERTLEIN & STRONG, 1946: 103-104

- TURNER, 1956: 69-70; 132 (plt. expl.); plt. 20, figs. 3, 4

- KEEN, 1958: 84-85; figs. 159, 160

- OLSSON, 1961: 181-182; 489 (plt. expl.); plt. 25, figs. 5-5d

- BRANN, 1966: 34 (plt. expl.); plt. 9, fig. 116 [as *Gouldia*]

- KEEN, 1971: 105-106; fig. 234

Astarte (*Crassinella*) *branneri* Arnold, 1903

- ARNOLD, 1903: 30, 60, 127-128; 398 (plt. expl.); plt. 18, fig. 12

[*Crassinella*]

- DALL, 1916: 24

- DALL, 1921: 31

- JORDAN, 1926: 244

- GRANT & GALE, 1931: 270

- JORDAN, 1936: 125

- BURCH, 1944: 9

- WOODRING, BRAMLETTE & KEW, 1946: 82; 136 (plt. expl.); plt. 36, figs. 1-6

- HERTLEIN & GRANT, 1972: 228-229; plt. 43, figs. 24, 25, 28, 29

Crassinella mexicana Pilsbry & Lowe, 1932

- PILSBRY & LOWE, 1932: 103-104; 144 (plt. expl.); plt. 14, figs. 8, 9

- HERTLEIN & STRONG, 1946: 104 [as a subspecies of *C. pacifica*]

- KEEN, 1958: 84-85; fig. 160 [as a subspecies of *C. pacifica*]

- OLSSON, 1961: 182; 489 (plt. expl.); plt. 25, fig. 4

- KEEN, 1971: 104-105; fig. 233

Crassinella quintinensis Manger, 1934

- MANGER, 1934: 298-299; 303 (plt. expl.); plt. 21, figs. 1, 2

- HERTLEIN & GRANT, 1972: 229 [as a synonym of *C. branneri*]

Type Material and Localities:

Gouldia pacifica — MCZ 186297, lectotype (restricted herein), left valve; length, 4.9 mm; height, 4.2 mm; thickness, 0.9 mm (Figure 1). This is the larger of the 2 valves selected by TURNER (1956) as a "lectotype," the right valve belonging to another specimen. MCZ 186298, paralectotypes (21 valves).

Panama Bay (about 8°57'N, 79°34'W); "Station. - - Unknown."; C. B. Adams, 1850

Astarte (*Crassinella*) *branneri* — USNM 162527, holotype, left valve; length, 11.2 mm (ARNOLD, 1903: 398). The specimen is now missing (J. Rosewater, letters of 24 March 1977 & 3 March 1978; T. R. Waller, letter of 10 January 1978).

Los Cerritos [Signal Hill], Los Angeles County, California (33°50'N, 118°10'W); late Pleistocene, "Upper San Pedro series" [Palos Verdes Sands]; D. & R. Arnold

Crassinella mexicana — ANSP 155622, holotype, left valve; length, 3.4 mm; height, 3.3 mm; thickness, 1.8 mm (Figure 2)

Guaymas, Sonora, Mexico (27°50'N, 110°54'W); about 37 m; H. N. Lowe, 1930

Crassinella quintinensis — Holotype, right valve; length, 7.9 mm; height, 7.5 mm; thickness, 2.3 mm (MANGER, 1934). Supposedly in the USNM, but it cannot be located there (T. R. Waller, letter of 19 January 1978), nor is it in Johns Hopkins University (S. M. Stanley, letter of 6 March 1978)

Bahía San Quintín, Baja California Norte, Mexico (32°21'N, 115°59'W); Johns Hopkins University (?) Locality 11729; Pleistocene

Description:

Shell ovate-trigonal, moderately compressed to somewhat inflated (length about 2.2 times thickness of paired valves), large among living members of genus (to 8 mm in material from Bahía Magdalena, Baja California Sur, LACM 71-14; to 10 mm in material from Golfo de Papagayo, Costa Rica, LACM 72-34; to 6 mm in material from the Gulf of Panama, LACM 72-55; to 11.2 mm in material from the Pleistocene of San Pedro, California, as

holotype of *Astarte (Crassinella) branneri*). Approximately equilateral in most to longer posteriorly in some (as CAS 17869; Isla Meanguera, El Salvador); anterior end rounded, slightly produced; posterior end angular, pointed (not rostrate as in *Crassinella ecuadoriana*); antero-dorsal margin slightly convex; postero-dorsal margin straight to slightly concave; ventral edge rounded. Beaks pointed, opisthogyrate. Exterior surface with irregular, rounded concentric ribs; sculpture more irregular toward ventral margin; interspaces generally wider than ribs; ribs sharper and narrower posteriorly; ribs capped with a lamella; exterior surface with conspicuous, fine radial rays and a faint "cellular" pattern. Lunule narrow, wider in left valve; escutcheon wide, wider in right valve. Shell white to light brown externally, often with brown radial rays, which are sometimes visible only on rib tops, giving shell a spotted appearance; white to brown within.

Right valve with a narrow, poorly defined cardinal tooth on proximal end of anterior lateral ridge. Main anterior cardinal tooth large; a large, triangular ligament posterior to it. Anterior end with a lateral ridge, an elongate anterior lateral tooth about $\frac{2}{3}$ of way to its distal end; ridge separated from sharp edge of lunule by a groove; margin of escutcheon rounded; an elongate lateral tooth present below posterior margin near posterior end of escutcheon.

Left valve with a large anterior cardinal widely separated from ligament; anterior margin of ligamental area raised, sometimes forming a low, narrow tooth; posterior cardinal present, congruent with proximal end of posterior lateral ridge; lunule with a sharp edge; a narrow, elongate lateral situated below anterior margin near anterior end of lunule; posterior edge with a lateral ridge separated from sharp edge of escutcheon by a groove and swollen into a lateral tooth near distal end.

Populations of this species differ in size and shape, but the greatest variability is in sculpture. Although most specimens have conspicuous sculpture, adults in some

areas are almost smooth. Typical specimens are shown in Figures 3 and 4.

Geographic Distribution and Habitat:

This species occurs from Crescent Bay, Laguna Beach, Orange County, California (33°32'48"N, 117°48'06"W) (LACM 11069), along the outer coast of Baja California, to and throughout the Gulf of California, and south to Zorritos, Tumbes Province, Peru (3°40'S, 80°40'W) (Paleontological Research Institution 25632; figured by OLSSON, 1961: pl. 25, fig. 5d). Depth records are from the low intertidal area to 158 m, with nearly all records in less than 40 m (mean depth, 24.5 m). Most labels on which a bottom type is noted indicate a sand substrate, but a few labels record mud substrates. I have seen 238 Recent lots.

Discussion:

The well known southern California Pleistocene *Crassinella branneri* must fall into the synonymy of *C. pacifica*. The only character that authors have noted to distinguish the two — a "narrower posterior ventral end" (HERTLEIN & GRANT, 1972: 229) — is within the range of variation of Recent material.

Crassinella pacifica is very similar to the Caribbean *C. lunulata* (Conrad, 1834). Both are variable in many features, and it is difficult to define the differences between them. *Crassinella lunulata* seems to average larger in size, to exhibit greater variability in sculpture, and to be smoother on an average than *C. pacifica*. In the future, workers may decide to regard the 2 as synonyms or as subspecies.

Crassinella oregonensis KEEN, 1938 (pp. 31-32; pl. 2, figs. 11, 12) was described from a single left valve (not right as originally supposed; KEEN, 1939: 252) obtained at Coos Bay, Oregon (CAS-SUPTC 6052) (Figure 5). It is apparently a stray valve of *C. lunulata* brought to

Explanation of Figures 7 to 12

Figure 7: *Crassinella ecuadoriana* Olsson. External view of right valve; LACM 63-11; Mazatlán, Mexico; length, 4.4 mm

Figure 8: *Crassinella nuculiformis* Berry, holotype, external and internal views (left valve); CAS-SUPTC 6570; early Pleistocene of San Pedro, California; length, 5.3 mm

Figure 9: *Crassinella nuculiformis* Berry. Holotype of *C. clementia* Pilsbry & Olsson; external views of both valves; ANSP 13714; Pliocene of Punta Blanca, Ecuador; length, 4.0 mm

Figure 10: *Crassinella nuculiformis* Berry. External view of right valve; LACM 69-21; south of Puertecitos, Baja California Norte, Mexico; length, 2.9 mm

Figure 11: *Crassinella nuculiformis* Berry. External view of right valve and internal view of both valves; CAS 59980; Cuastecomate, Mexico; length, 4.5 mm

Figure 12: *Crassinella skoglundae* Coan, spec. nov., holotype; external and internal views of both valves; CAS 59931; La Cruz, Bahía Banderas, Mexico; length, 5.5 mm



Figure 7

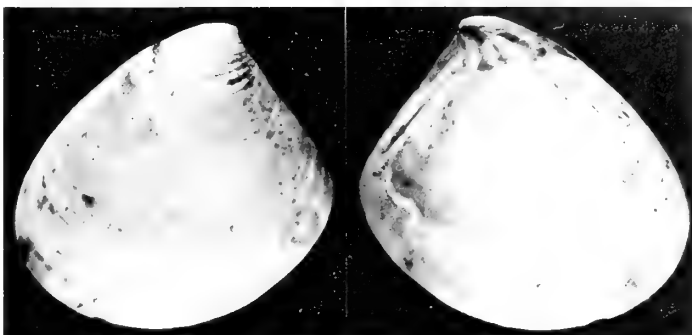


Figure 8



Figure 10

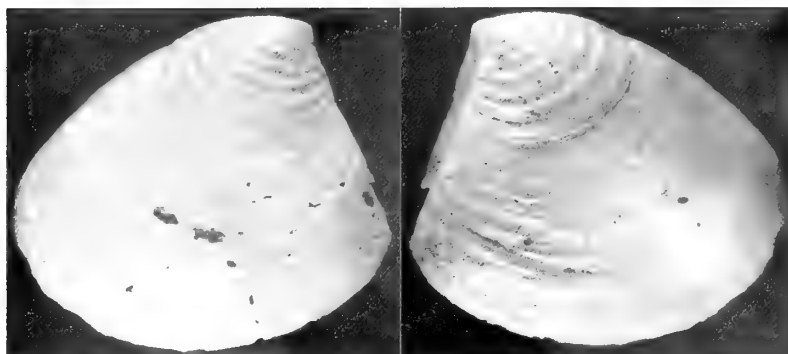


Figure 9

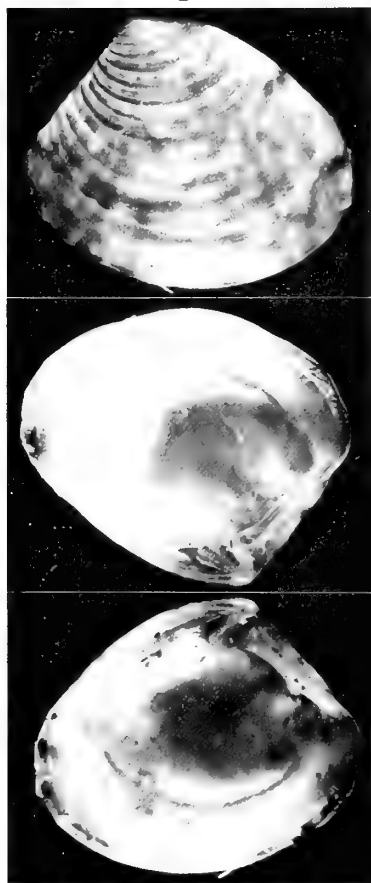


Figure 11

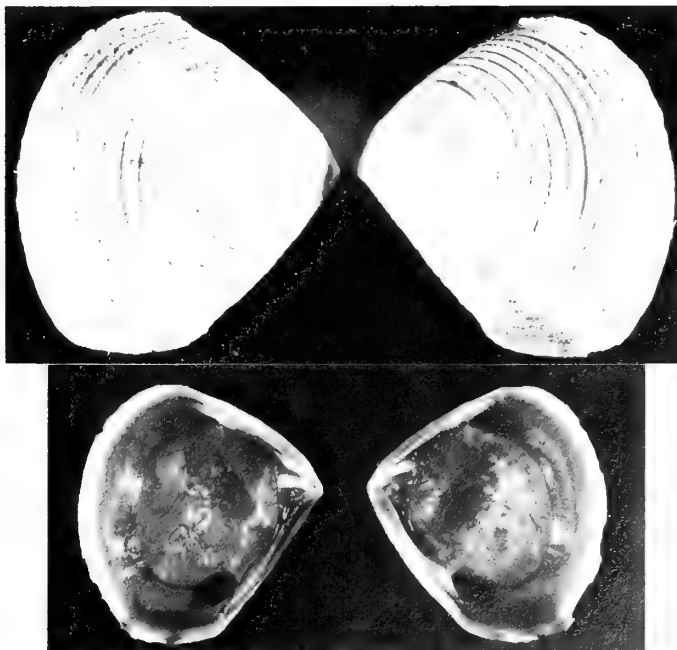


Figure 12

that locality with a shipment of oysters for mariculture (J. T. Carlton, letter to B. Roth, 12 January 1977).

What is recorded from the Miocene Altamira shale of San Pedro, California, as "*Crassinella* cf. *C. mexicana* Pilsbry and Lowe" by WOODRING, BRAMLETTE & KEW (1946: 27, 128; plt. 28, fig. 12) is uncertain.

Crassinella ecuadoriana Olsson, 1961

(Figures 6, 7)

Crassinella ecuadoriana Olsson, 1961

OLSSON, 1961: 182-183; 498 (plt. expl.); plt. 25, figs. 6-6e
KEEN, 1971: 104-105; fig. 232

Type Material and Locality:

ANSP 218934, holotype, pair; length, 2.9 mm; height, 2.5 mm; thickness, 1.4 mm (Figure 6). ANSP 218934a, paratypes (5)
Puerto Callo, Manabi Province, Ecuador (1°20'30"S, 80°14'30"W); A. A. Olsson

Description:

Shell lunate, moderately inflated (length 2.4 times thickness of paired valves), medium in size for genus (to 4.6 mm; LACM 70-9). Length about 1.2 times height. Approximately equilateral; anterior end rounded; posterior end produced, rostrate; antero-dorsal margin weakly concave; postero-dorsal margin strongly concave; ventral edge rounded. Beaks pointed, opisthogyrate. Exterior surface with conspicuous concentric ribs, narrow and widely spaced dorsally, broad and closer together ventrally; ribs with a narrow lamella on their tops; ribs sharper posteriorly. Exterior surface with fine radial rays and a minute "cellular" pattern. Lunule narrow, slightly wider in left valve; escutcheon wide, wider in right valve. Interior white to brown; exterior surface brown or purple, sometimes with brown radial rays.

Right valve with a narrow, inconspicuous cardinal on proximal end of anterior lateral ridge. A second, large, curved anterior cardinal situated close to ligament; anterior end with a lateral ridge separated from sharp border of lunule by a groove; anterior ridge with a small lateral tooth about $\frac{2}{3}$ of way to its distal end; escutcheon with a rounded edge; a weak posterior lateral ridge with a small lateral tooth on it within postero-dorsal margin near posterior end of escutcheon.

Left valve with a large, curved anterior cardinal, with a small, thin cardinal between it and ligament; a posterior cardinal behind ligament attached to proximal end of posterior lateral ridge; posterior lateral ridge with a

large, distal tooth; weak anterior lateral ridge with a small lateral tooth on it within antero-dorsal margin near anterior end of lunule.

A typical specimen is shown in Figure 7.

Geographic Distribution and Habitat:

La Paz, Baja California Sur (24°10'N, 110°19'W) (CAS 59413), and Mazatlán, Sinaloa, Mexico (about 23°12'N, 106°25'W) (*e. g.*, USNM 566508), to the SE side of Punta Ancón, Guayas Province, Ecuador (2°20'S, 80°53'30"W) (LACM 70-12). Depth records are from the low intertidal area to 55 m, with most records in less than 25 m (mean depth, 13 m). The bottom types noted on some labels suggest that the species prefers a sandy or rocky substrate. I have studied 57 lots.

Crassinella nuculiformis Berry, 1940

(Figures 8 to 11)

Crassinella nuculiformis Berry, 1940

BERRY, 1940: 3-5; 16 (plt. expl.); plt. 1, figs. 1, 2

BURCH, 1944: 9

WOODRING, BRAMLETTE & KEW, 1946: 82; 136 (plt. expl.); plt. 36, figs. 7-10

Crassinella clementia Pilsbry & Olsson, 1941

PILSBRY & OLSSON, 1941: 56-57; 78 (plt. expl.); plt. 12, fig. 8

Type Material and Localities:

Crassinella nuculiformis — CAS-SUPTC 6570, holotype, left valve [not right, as Berry supposed]; length, 5.3 mm; height, 4.4 mm; thickness, 1.3 mm (Figure 8). CAS-SUPTC 6570a, paratypes (2 valves)

San Pedro, Los Angeles County, California; west side of Gaffey Street, "in cut just below General Street" [should be General Avenue] (33°44'54"N, 118°17'30"W); early Pleistocene; San Pedro Sand; S. S. Berry & R. K. Cross

Crassinella clementia — ANSP 13714, holotype, paired valves (sealed); length, 4.0 mm; height, 3.6 mm; thickness, 1.6 mm (Figure 9). ANSP 13714a, paratype (1 valve)

Punta Blanca, about 8.5 km S of Cabo San Lorenzo, Manabi Province, Ecuador (1°07'30"S, 80°53'30"W); Canoa Formation; Pliocene; A. A. Olsson, 1936-1938

Description:

Shell ovate-cuneiform, shape reminiscent of a venerid or a nuculid, moderately inflated (length about 2.3 times thickness of paired valves), medium in size for genus (to 6.4 mm; LACM 60-20). Length about 1.25 times height. Anterior end longer, rounded; posterior end somewhat

acute; antero-dorsal margin slightly convex; postero-dorsal margin straight; ventral margin rounded. Beaks pointed, decidedly opisthogyrate. Exterior surface with concentric ribs concentrated near beaks; surface smoother ventrally; interspaces as wide or wider than ribs; ribs sharper, more raised posteriorly; exterior surface with fine radial rays and a fine "cellular" pattern. Lunule longer than escutcheon, narrow, approximately equal in the 2 valves; escutcheon wide, approximately equal in the 2 valves. Shell brownish within; externally with brown rays or mottling.

Right valve with a narrow anterior cardinal congruent with anterior lateral ridge; a large anterior cardinal posterior to narrow cardinal; triangular ligament immediately posterior to large cardinal, its posterior margin sometimes raised into a ridge. Sharp edge of lunule bordered by a groove, defining a rounded anterior lateral ridge; anterior ridge with an elongate lateral tooth distally; escutcheon bordered by a rounded ridge; a weak internal posterior lateral ridge sometimes present.

Left valve with a large anterior cardinal; ligament separated from this cardinal by a short gap; gap with a small, thin, low cardinal. A ventrally directed posterior cardinal immediately posterior to ligament. Lunule bordered by a rounded ridge. A weak internal anterior lateral ridge sometimes present. Sharp edge of escutcheon bordered by a groove, separating off a rounded internal ridge, which is swollen into a lateral tooth distally.

There is some variability in the relative height of specimens. The greatest variability is in the degree to which the concentric ribs cover the shell surface. In some individuals, they are confined to the area near the beaks; in others, they extend most of the way to the ventral margin. Color is also variable; some specimens have only traces of brown mottling; others have narrow radial bands; still others have fairly wide brown bands. Worn material is yellow, rather than brown. Material from the head of the Gulf of California referred to this species (Figure 10) is smaller in size (generally less than 3 mm

in length) and shorter posteriorly than material from further south. A typical specimen from central Mexico is shown in Figure 11.

Geographic Distribution and Habitat:

From the northeast end of Isla Cedros, Baja California Norte, Mexico ($28^{\circ}20'25''N$, $115^{\circ}11'20''W$) (LACM 71-152), to and throughout the Gulf of California, south to the Gulf of Guayaquil, Guayas Province, Ecuador (SW of Playas; $2^{\circ}49'S$, $80^{\circ}31'W$) (LACM 66-193). This species occurs from the low intertidal area to about 62 m, with most records in less than 40 m (mean depth, 20 m). Most labels on which bottom type is recorded note a sand substrate, but some suggest that the species is also found on muddy and rocky substrates. I have examined 65 Recent lots.

Crassinella skoglundae Coan, spec. nov.

(Figures 12 to 15)

Description of Holotype and Measured Paratypes:

Shell high, triangular, moderately inflated (holotype length 1.96 times thickness; mean of measured type specimens, 2.06), large among living members of genus (to 6.8 mm; CAS 59418). Length averaging 1.11 times height. Anterior end weakly acuminate; posterior end longer, somewhat truncate; antero-dorsal margin straight to slightly convex; postero-dorsal margin straight; ventral edge evenly rounded. Beaks pointed, weakly opisthogyrate. Exterior surface with even, rounded concentric ribs; ribs moderately wide, equal to or slightly wider than interspaces, narrower and raised anteriorly; exterior surface with an obscure radial pattern and a still fainter "cellular" pattern. Lunule moderate in width, wider in right valve; escutcheon as long as lunule and

Explanation of Figures 13 to 18

Figure 13: *Crassinella skoglundae* Coan, spec. nov., paratype I; external view of right valve; CAS 59932; same locality as holotype; length, 5.9 mm

Figure 14: *Crassinella skoglundae* Coan, spec. nov., paratype II; external view of right valve; CAS 59933; same locality as holotype; length, 5.5 mm

Figure 15: *Crassinella skoglundae* Coan, spec. nov., paratype III; external view of right valve; CAS 59934; same locality as holotype; length, 5.5 mm

Figure 16: *Crassinella adamsi* Olsson, holotype; external and internal views (left valve); ANSP 218933; Punta Blanca, Ecuador; length, 3.6

Figure 17: *Crassinella adamsi* Olsson. External and internal views of both valves; CAS 59981; Bahía Audiencia, Manzanillo, Mexico; length, 2.9 mm

Figure 18: *Crassinella varians* (Carpenter), lectotype (herein); external and internal views (left valve); BM[NH] Carpenter Mazatlán Collection 1857.6.4.416; Mazatlán, Mexico; length, 2.05 mm

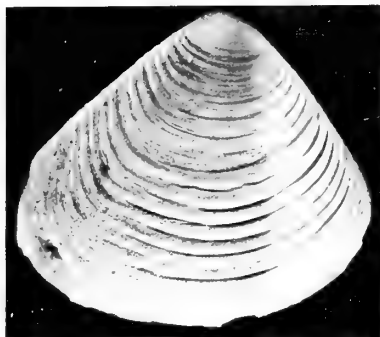


Figure 13

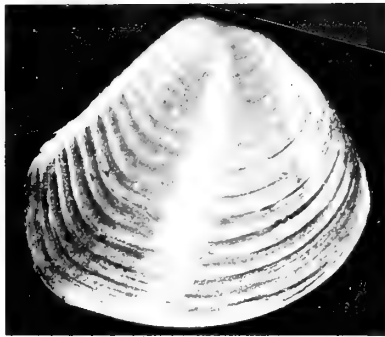


Figure 14



Figure 15

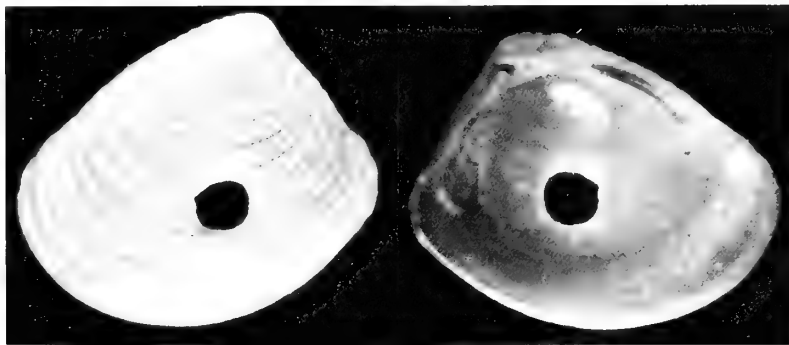


Figure 16

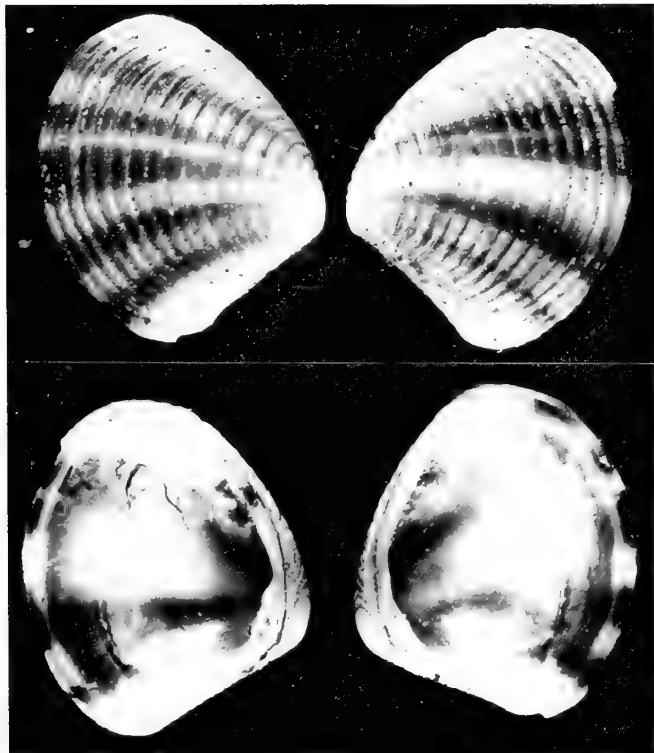


Figure 17

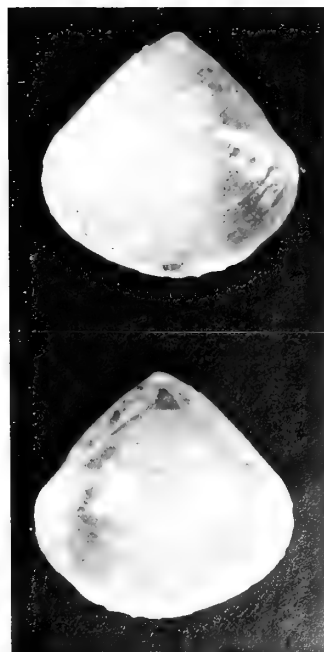


Figure 18

wider, widest in right valve. External surface of holotype with 2 narrow brown radial bands on its posterior slope; purplish-brown within.

Right valve with a thin cardinal on proximal end of anterior lateral ridge; a large anterior cardinal situated next to ligament (sometimes with a smaller, thinner, lower cardinal between large anterior cardinal and ligament); anterior end with a lateral ridge separated from sharp edge of lunule by a groove and with an elongate lateral tooth about $\frac{3}{8}$ of way to distal end; margin of escutcheon rounded. Posterior end sometimes with a low internal lateral ridge.

Left valve with a large anterior cardinal widely separated from ligament; anterior margin of ligamental area raised, sometimes forming a low, narrow tooth; gap posterior to ligament; posterior cardinal on proximal end of posterior lateral ridge; posterior end with a lateral ridge separated from shell margin by a groove and with an elongate lateral tooth about $\frac{3}{8}$ of way to distal end; anterior margin rounded, sometimes with a low internal lateral ridge.

Type Material:

Type material	# in CAS	Figure herein	Length (l)	Height (h)	l/h	Thickness (th)	l/th
Holotype	59931	12	5.5 mm	5.2 mm	1.06	2.8 mm	1.96
Paratype I	59932	13	5.9	4.9	1.20	2.8	2.11
Paratype II	59933	14	5.5	5.2	1.06	2.8	1.96
Paratype III	59934	15	5.5	4.9	1.12	2.5	2.20
Means					1.11		2.06
					(SD = 0.07)		(SD = 0.12)

Paratypes have also been placed in the Los Angeles County Museum of Natural History, U. S. National Museum of Natural History, Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Museum of Comparative Zoology, and San Diego Natural History Museum.

Type Locality:

La Cruz, Bahía Banderas, Nayarit, Mexico ($20^{\circ}45'N$, $105^{\circ}24'W$); 7.5 to 15 m; mud; Carol and Paul Skoglund; 31 July 1973.

Variation Among Type Specimens:

The type lot contains 29 complete individuals ranging in size from 2 to 5.9 mm. Paratype I differs from the

holotype in having a somewhat less rounded ventral margin and in having an entirely brown posterior end, rather than 2 narrow brown radial bands (Figure 13). It is unique among the material studied of this and other species in having posterior and anterior lateral ridges in the left valve and no ridges in the right valve. Paratype II differs from the holotype in having broad brown radial bands, one on the posterior slope and one on the anterior slope (Figure 14). Paratype III differs from the holotype in having a more sharply quadrate posterior end; its posterior slope shows only obscure brownish areas extending half way from the ventral margin towards the beaks (Figure 15).

There seems to be less sculptural variation among specimens of this species than with most other west American members of the genus. However, in some specimens, the ribbing is a little heavier; in others it is finer and more numerous.

Comparisons:

Crassinella skoglundae differs from all other eastern Pacific species in having a shorter anterior end. Some populations of *C. pacifica* in Central America have a relatively

short anterior end, but these specimens may be easily distinguished from the new species by their irregular lamellar sculpture. All specimens of *C. skoglundae* studied have even, rounded concentric ribs.

Crassinella skoglundae differs from *C. nuculiformis* not only in having a shorter anterior end but in being proportionately higher and in having concentric ribs over the entire shell surface.

Geographic Distribution and Habitat:

From La Cruz, Bahía Banderas, Nayarit, Mexico ($20^{\circ}45'N$, $105^{\circ}24'W$), to Acapulco, Guerrero ($16^{\circ}51'N$, $99^{\circ}56'W$; CAS 27202), Mexico. Depth records are from 11 to 28 m (mean, 18 m). The species has been recorded from both mud and gravel bottoms and is known from 8 lots.

Crassinella adamsi Olsson, 1961

(Figures 16, 17)

Crassinella adamsi Olsson, 1961

OLSSON, 1961: 183; 498 (plt. expl.); plt. 25, figs. 3-3e

KEEN, 1971: 104-105; fig. 231

Type Material and Locality:

ANSP 218933, holotype, left valve; length, 3.6 mm; height, 3.0 mm; thickness, 1.0 mm (Figure 16). ANSP 218933a, paratypes (4)

Punta Blanca, about 8.5 km S of Cabo San Lorenzo, Manabí Province, Ecuador (1°07'30"S, 80°53'30"W); A. A. Olsson

Description:

Shell ovate, inflated (length 1.75 times thickness of paired valves), small among members of genus (to 3.6 mm; holotype). Length about 1.2 times height. Anterior end longer, rounded; posterior end somewhat angular; antero-dorsal margin slightly convex; postero-dorsal margin weakly concave; ventral edge convex. Beaks rounded, decidedly opisthogyrate. Exterior surface with heavy concentric ribs; ribs more than twice width of interspaces, rising steeply on their dorsal side, sloping more gradually on their ventral side; ribs higher near dorsal shell surface than ventrally, narrower posteriorly. Exterior surface with fine radial lines and a "cellular" pattern. Lunule narrow, wider in left valve; escutcheon wide, wider in left valve. Shell light brown within; externally light brown, often with irregular, darker brown rays, narrow in some specimens, broad in others.

Right valve with a large anterior cardinal; triangular ligament immediately posterior to anterior cardinal; ligament with a raised posterior border; a deep pit (for peg-like cardinal of left valve) posterior to ligament; anterior end with a narrow ridge, separated from shell margin by a groove; posterior margin sharp.

Left valve with an elongate, oblique anterior cardinal; a thin, narrow cardinal just anterior to triangular liga-

ment; a short peg-like cardinal immediately posterior to ligament. Edge of lunule rounded, with an inconspicuous lateral tooth below shell margin near anterior end of lunule; edge of escutcheon separated from a thin lateral ridge by a groove.

A typical specimen is shown in Figure 17.

Geographic Distribution and Habitat:

Mazatlán, Sinaloa, Mexico (23°12'N; 106°25'W) (CAS 27223), to Gulf of Guayaquil, Guayas Province, Ecuador (SW of Playas; 2°49'S; 80°31'W) (LACM 66-193). Depth records are from 9 to 100 m, with most records in less than 40 m (mean depth, 31 m). The only bottom type recorded is sand. I have examined 20 lots.

OLSSON (1961) mentions a similar, as yet undescribed Caribbean species, which differs in having deeper interspaces between the concentric ribs.

Crassinella varians (Carpenter, 1857)

(Figures 18 to 20)

Gouldia varians Carpenter, 1857CARPENTER, 1857a: 247, 306, 364, 366 [*nomen nudum*]

CARPENTER, 1857b: 83-84, 86, 530, 549

[*Crassatella*]

CARPENTER, 1864b: 544, 620 [1872: 30, 106]

[*Crassatella* (*Crassinella*)]LAMY, 1917: 248-249 [as "var" of *C. pacifica*][*Crassinella*]

BURCH, 1944: 9, 18

HERTLEIN & STRONG, 1946: 104

WOODRING, BRAMLETTE & KEW, 1946: 82

KEEN, 1958: 84

OLSSON, 1961: 183; 498 (plt. expl.); plt. 5, figs. 7-7b

BRANN, 1966: 34 (plt. expl.); plt. 9, fig. 117 [as *Gouldia*]

KEEN, 1968: 393; 394 (plt. expl.); 395, figs. 2a, 2b

KEEN, 1971: 105-106; fig. 235

Crassinella goldbaumi Jordan, 1936

JORDAN, 1936: 112, 126; 166 (plt. expl.); plt. 18, figs. 4, 5

Explanation of Figures 19 to 22

Figure 19: *Crassinella varians* (Carpenter). Holotype of *C. goldbaumi* Jordan; CASGTC 5586; external and internal views (left valve); Pleistocene of Bahía Magdalena, Baja California Sur; length, 3.3 mm

Figure 20: *Crassinella varians* (Carpenter). External and internal views of both valves; LACM 72-19; Bahía Jobo, west of Bahía de Salinas, Costa Rica; length, 2.8 mm

Figure 21: *Crassinella coxa* Olsson, holotype, external and internal views (left valve); USNM 644100; Pleistocene of Quebrada Camarones, Ecuador; length, 2.3 mm

Figure 22: *Crassinella coxa* Olsson. External and internal views of both valves; LACM 72-34; Islas Huevos, Costa Rica; length, 2.3 mm

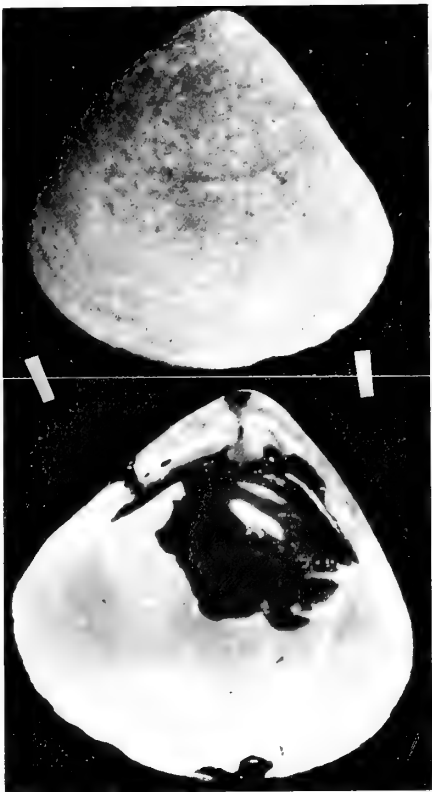


Figure 19

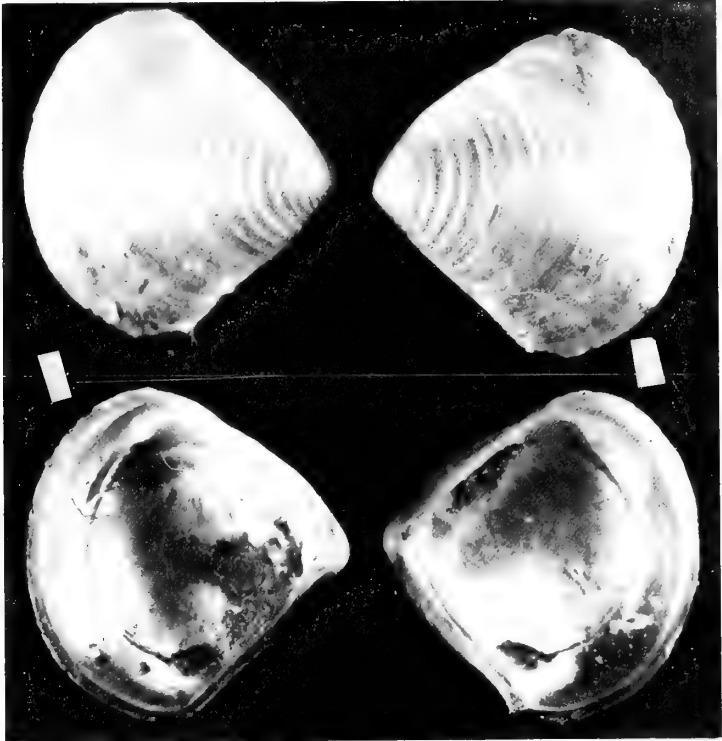


Figure 20



Figure 21

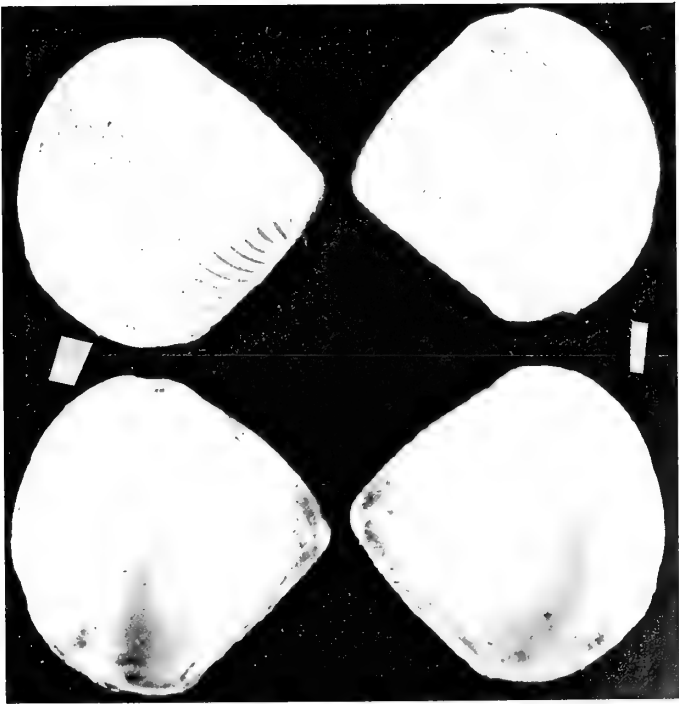


Figure 22

Crassinella haylocki Pilsbry & Olsson, 1941

PILSBRY & OLSSON, 1941: 57; 79 (plt. expl.); plt. 18, figs. 7, 8

Type Material and Localities:

Gouldia varians — BM(NH) Carpenter Mazatlán Collection #1857.6.4.416, lectotype (herein), left valve; length, 20.5 mm; height, 2.0 mm (Figure 18). Paralectotypes: also in Tube 416 [corresponds to Carpenter Tablet #]: 3 valves; Tube 415: 1 small pair, 9 valves, 2 disintegrated valves; Tablet 417: 2 disintegrated valves, 1 semi-disintegrated valve; Tablet 418: 2 disintegrated valves, 1 broken valve; Tube 419: 4 valves, 1 disintegrated valve

Mazatlán, Sinaloa, Mexico (23°12'N, 106°25'W); in "shell washings"; F. Reigen

Crassinella goldbaumi — CASGTC 5586, holotype, left valve [not right as stated by Jordan]; length, 3.3 mm; height, 3.2 mm; thickness, 1.0 mm (Figure 19). CASGTC 5587, 5587a, 5587b, 5587c, paratypes

California Academy of Sciences locality 754, just N of the village of Bahía Magdalena, Baja California Sur, Mexico (24°38'N, 112°09'W); Pleistocene; G. D. Hanna & E. K. Jordan, 1925

Crassinella haylocki — Holotype, right valve; length, 2.6 mm; height, 2.5 mm; thickness, 0.6 mm (PILSBRY & LOWE, 1941: 57) This specimen cannot be located in the ANSP (E. V. Scott, letter of 8 November 1977)

Punta Blanca, about 8.5 km S of Cabo San Lorenzo, Manabí Province, Ecuador (1°07'30"S, 80°53'30"W); Canoa Formation; Pliocene; A. A. Olsson, 1936-1938

Description:

Shell high, triangular, inflated (length about 1.7 times thickness of paired valves), small for genus (to 3.2 mm; USNM 268977). Length averaging 0.97 times height. Shell nearly equilateral to slightly longer posteriorly; anterior end rounded; posterior end subangular; antero-dorsal margin weakly convex; postero-dorsal margin almost straight; ventral edge rounded. Beaks rounded, not conspicuously opisthogyrate. Exterior surface with very low concentric ribs, strongest and narrowest near beaks, becoming wider and less evident near anterior margin. Some specimens nearly smooth. The surface "cellular" pattern very fine, scarcely evident; radial pattern even less evident. Lunule fairly wide, widest in left valve; escutcheon still wider, widest in right valve. Shell brown, purple, or white within; brown or white externally, very often with a broad, dark band on anterior slope.

Right valve with a large, straight anterior cardinal and a triangular ligament between it and a small posterior cardinal; anterior margin separated from a lateral ridge by a groove; proximal end of this ridge raised into a cardinal tooth; ridge also often swollen into a lateral tooth about $\frac{2}{3}$ of way to its distal end; posterior margin

sharp, with a notch near beaks for posterior cardinal of left valve.

Left valve with an anterior cardinal separated from triangular ligament by a space; ligament with a slightly raised anterior border; a short, projecting posterior cardinal connected to posterior lateral ridge; margin of lunule rounded; posterior margin separated by a groove from lateral ridge, often swollen into a lateral tooth about $\frac{2}{3}$ of way to its distal end.

As the specific name implies, *Crassinella varians* exhibits variability in several features. Some specimens are longer posteriorly than others. However, sculpture is the most variable feature; some specimens are almost smooth, others covered with the characteristic low concentric ribs. Whereas a broad brown anterior band is typical, some specimens are entirely white or entirely brown. A typical specimen is shown in Figure 20.

Geographic Distribution and Habitat:

From Bahía San Juanico, Baja California Sur (26°15'N; 112°27'20"W) (LACM 71-180), to and throughout the Gulf of California, and south to the Gulf of Guayaquil, Guayas, Ecuador (SW of Playas; 2°49'S; 80°31'W) (LACM 66-193), and the Galápagos Islands (off Isla Española; USFC Stn. 2813; 1°21'S; 89°40'15"W) (USNM 195042). This species occurs from the low intertidal area to about 113 m, with most records in less than 40 m (mean depth, 28 m). Most labels on which a bottom type is recorded note a sand substrate, but a few suggest that the species is also found on mud. I have examined 67 Recent lots.

Crassinella coxa Olsson, 1964

(Figures 17, 18)

Crassinella coxa Olsson, 1964

OLSSON, 1964: 43; 212 (plt. expl.) [as "coxi"]; plt. 5, figs. 11, 12

Type Material and Locality:

USNM 644100, holotype, left valve; length, 2.3 mm; height, 2.3 mm; thickness, 0.8 mm (Figure 17). USNM 644101, paratype (left valve). (The labels in Olsson's writing have the "coxa" spelling.)

Quebrada Camerones, about 10 km E of Río Esmeraldas, Esmeraldas Province, Ecuador (1°00'N, 79°37'W); Esmeraldas Formation; Pleistocene

Description of Recent Material:

Shell triangular, inflated (length about 1.6 times thickness of paired valves), small for genus (to 2.9 mm length; LACM 72-34). Length about 1.13 times height. Nearly equilateral to a little longer posteriorly; anterior end rounded; posterior end subangular; antero-dorsal slope slightly convex; postero-dorsal margin weakly convex; ventral margin deeply rounded. Beaks pointed, slightly opisthogyrate. Exterior surface with conspicuous, raised concentric ribs; ribs slightly narrower than interspaces; ribs often weaker on posterior slope in a triangular patch extending from ventral margin to a point about $\frac{2}{3}$ of way to beaks and also weaker just below lunular margin; radial and "cellular" pattern weak, but stronger than in *Crassinella varians*. Lunule fairly wide, widest in left valve; escutcheon still wider, widest in right valve. Shell white within and without.

Hinge as in *Crassinella varians*.

This species is close to *Crassinella varians*, and I have had some difficulty in assigning a few lots to one or the other. It seems to prefer deeper water than *C. varians*, and it is most easily recognized by its heavier sculpture and pure white color. It is slightly more convex and a little broader than *C. varians*. A typical Recent specimen is shown in Figure 18.

Geographic Distribution and Habitat:

From off Punta Rompiente, outer coast of Baja California Sur, Mexico (27°42'N; 115°05'W) (LACM 71-167); Isla Coronados, in the Gulf of California, Baja California Sur (26°07'15"N; 111°18'15"W) (AMNH 187086); and Bahía San Ignacio, Sinaloa, Mexico (25°26'N; 109°27'W) (LACM AHF2057), south to Puerto Utría, Chocó Province, Colombia (5°57'N; 77°21'W) (LACM AHF543).

This species is recorded from about 36 to 160 m (mean, 76.7 m). The only bottom type recorded is coarse sand. I have seen 8 Recent lots.

Another Species?

There is a single valve in the USNM (USNM 207621) from off the Galápagos Islands (USFC Stn. 2808) that appears to be close to the Caribbean *Crassinella martiniensis*. This station was in deep water (1158 m), deeper than any other record for the genus, and perhaps the valve came from drift or sampler contamination. This form should be looked for in shallower water in that area.

ACKNOWLEDGMENTS

My gratitude is extended to Mr. Barry Roth for his long-standing interest in this genus; his insights and suggestions have been of immeasurable value. Particular thanks are extended to Mr. Bertram C. Draper for his excellent photographs. I am also indebted to Ms. A. Blake, Dr. Kenneth J. Boss, Dr. James T. Carlton, Dr. William K. Emerson, Dr. Harold Harry, Mr. Patrick I. LaFollette, Dr. James H. McLean, Ms. Mary Jane Murphy, Dr. Robert Robertson, Dr. Joseph Rosewater, Ms. Elizabeth V. Scott, Mrs. Carol C. Skoglund, Dr. Steven M. Stanley, Dr. Thomas R. Waller, and Dr. Wendell P. Woodring for the loan of specimens, information about type specimens and localities, or other information. I appreciate the help of Mrs. Berenice Coan in recording some of the data, and of Dr. A. Myra Keen and Mr. Michael G. Kellogg in criticizing the manuscript.

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Short Account of the Anatomy of a Nudibranchiate Mollusk, *Aeolidiella takanosimensis* Baba, 1930 from Japan

(Eolidoidea : Aeolidiidae)

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(6 Text figures)

THE SPECIES, *Aeolidiella takanosimensis*, was established by BABA, 1930, on the specimens collected from Tateyama Bay, Boshu ($34^{\circ}59'N$; $139^{\circ}50'E$). It was then presumed to be referable to *Eolis* sp. of IJIMA, 1918 shown in his book by an outline of the animal. Fortunately, *A. takanosimensis* was rediscovered by different authors (BABA, 1949; BABA & HAMATANI, 1952; ABE, 1964; INABA, 1963; USUKI, 1969; etc.) from a number of stations situated on the east and west coasts of the lower half of Japan, the southernmost limit of location being Tomioka of Amakusa ($32^{\circ}31'N$; $130^{\circ}02'E$). Moreover, there occurred latest records of this species in the Mediterranean Sea (SCHMEKEL, 1968; 1970) and the west coast of North America (San Diego and Los Angeles counties by SPHON, 1971; and Baja California del Sur by FERREIRA & BERTSCH, 1975).

Here *Aeolidiella takanosimensis* is separated from *A. multicolor* Macnae, 1954 from False Bay, South Africa by the slight difference visible in the composition of the first several branches of the left posterior liver on the right side (see also MARCUS & MARCUS, 1967: 117).

The present study concerns the general morphology of *Aeolidiella takanosimensis* explored at different stations in Japan. However, I was indebted to Mr. Iwao Hamatani of the Tennoji Senior High School, Osaka Kyoiku University, for dissecting the liver system of the animal for illustration. My thanks are also due to those persons who helped me in collecting part of the specimens from shores.

Aeolidiella takanosimensis Baba, 1930

(Japanese name: Mino-umiushi)

(Figures 1-6)

Main Synonymy:

Aeolidiella takanosimensis BABA, 1930: 122, 124; pl. 4, figs. 5a-5c; text figs. 4a-4b. - Takanoshima, Tateyama Bay. BABA, 1949: 111-112, 183-184; pl. 49, fig. 167; text figs. 154-155. - Sagami Bay. ABE, 1964: 72-73; pl. 36, fig. 129. - Sado Island, Toyama Bay and vicinity. SCHMEKEL, 1970: 155-156. - Naples (genitalia). FERREIRA & BERTSCH, 1975: 329, fig. 19. - Baja California del Sur.
Eolidina (Eolidina) takanosimensis. BABA, 1937: 336 (generic name change).

Localities in Japan: Tateyama Bay; Tokyo Bay; Sagami Bay; Sugashima, Shima; Seto, Kii; Osaka Bay; The Inland Sea of Seto; Saeki Bay; Amakusa; Fukaura; Sado Island; Toyama Bay and vicinity

Distribution in the World: The Mediterranean Sea; East Pacific Ocean.

Main Material Examined:

Specimen no. 1: Sugashima, Shima, 9 April 1951
Specimen no. 2: Seto, Kii, 12 January 1971

- Specimen no. 3: Ohkawa, Osaka Bay, 20 August 1959
(dissected by Hamatani for the liver system)
- Specimen no. 4: Tomogashima, Osaka Bay, 6 May 1962 (prepared in horizontal serial sections)
- Specimen no. 5: Mukaishima, the Inland Sea of Seto, 29 March 1964
- Specimen no. 6: Ohnyu-jima, Saeki Bay, 2 and 4 April 1957
- Specimen no. 7: Tomioka, Amakusa, 21 May 1974
- Specimen no. 8: Ogi, Toyama Bay, 6 August 1960 (prepared in horizontal serial sections)
- Specimen no. 9: Ojima near Tojinbo, Echizen Coast, 12 August 1977

Description:

External Form: The animals collected for this study are generally small, and range from 6 to 13 mm in total length (the type specimens of *Aeolidiella takanosimensis* were 17 to 30 mm long while the 2 specimens recorded by Ferreira & Bertsch from Baja California del Sur measured 40 mm in length). The rhinophores are always smooth; they do not bear perfoliations that were noted on the preserved specimens of *Aeolidiella* (?*takanosimensis*) of RISBEC, 1956: 31-32 from Viet Nam. This latter form was renamed *Spurilla risbeci* by MARCUS, 1961: 56. The foot corners are angulated. The tail is moderately extended behind.

In Specimen no. 3 there are 23 to 25 rows of papillae on the back margins, of which the anteriormost 6 to 7 rows are to be attributed to the right liver (and the left partner), and the rest to the left posterior liver. The papillar arrangement after EDMUNDS, 1970 is as follows (Hamatani's observation): 5, 7, 8, 7, 8, 8, 2; 4, 5, 5, 3; 5, 5, 2, 2; 4, 1, 2; 4, 3; 3, 2, 2, 1, 1 on the right side, and 2, 3, 6, 6, 5, 7; 6, 5, 5, 4; 3, 4, 5; 2, 3; 2, 3; 2, 2, 1, 1, 1 on the left side. The cleioproctic anus opens on the right side within the first group of rows belonging to the left posterior liver. However, the anus tends to be pleuroproctic in situation as observed in Specimens nos. 2, 6 and 8, separately. A pleuroproctic position of the anus is also recorded from a paratype of *Cerberilla albopunctata* BABA, 1976: 276. The nephroproct lies closely in front of the anus. The genital orifices are found under anterior rows of the right liver rows. The branchial papillae themselves are contractile, and long or short fusiform according to their state of movement. They are not flattened.

In *Aeolidiella takanosimensis* the first rows of the branchial papillae on each side of the body do not appear to form a cephalic crown ("collerette céphalique") that was called attention to by TARDY, 1969 from some Atlantic

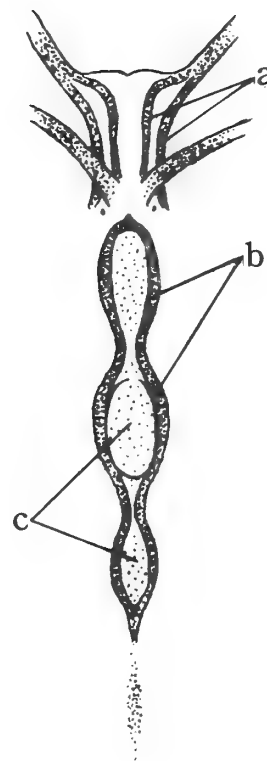


Figure 1

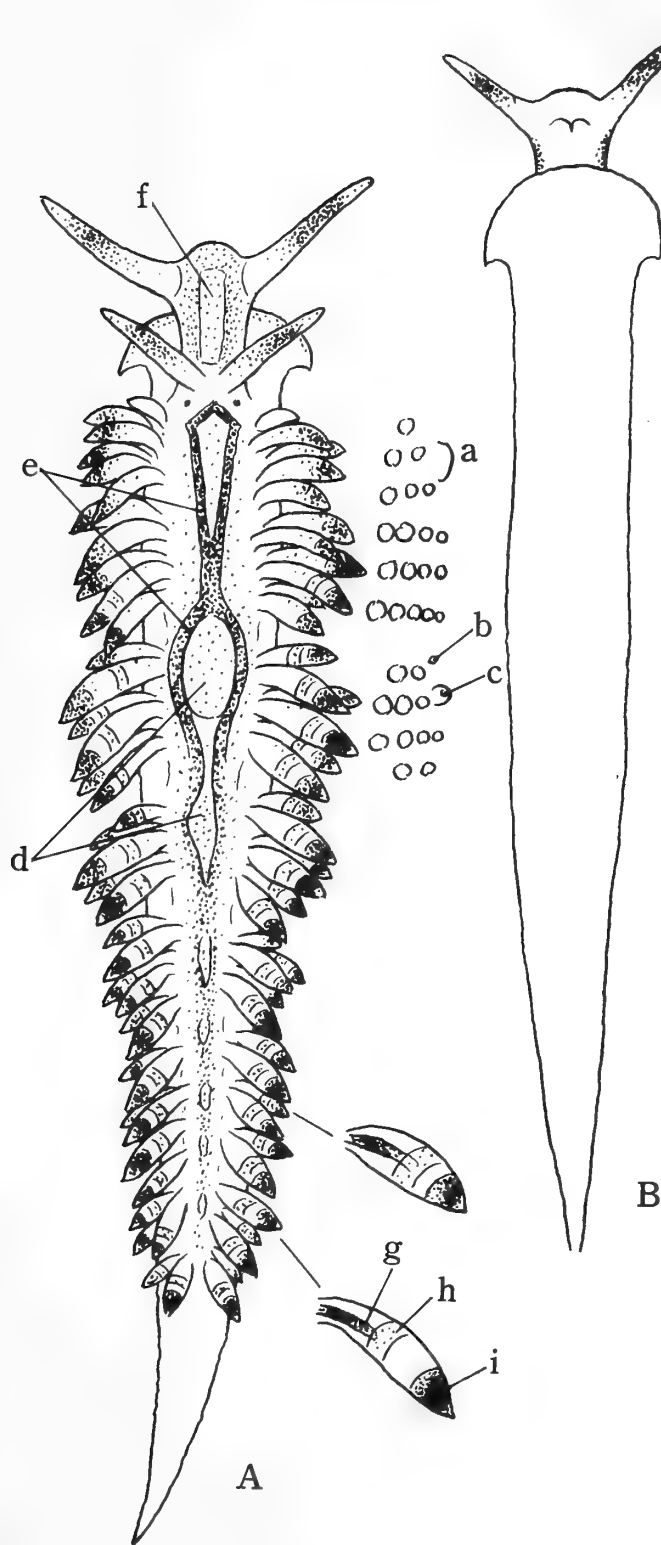
Aeolidiella takanosimensis Baba, 1930

Specimen no. 6, length 15 mm

Normal patterns of vermilion on the head (a) and back (b), and opaque white patches (c) in the median dorsal line

species of *Aeolidiella* (i.e., *A. glauca*, *A. alderi* and *A. sanguinea*).

Coloration: *Aeolidiella takanosimensis* is especially characterized by the possession of vermilion-tinted figures on the head and back. The formation of these figures, however, differs according to specimens. Usually there is a U-shaped letter (or a U-letter broken below) of vermilion on the head in the median line. The sides of the head are vermilion. The pericardial region is surrounded by a vermilion-tinted, oval or rhomboidal figure, the 2 horns of which extend forward to the bases of the rhinophores and often are united transversely. This vermilion figure passes back in the median line for some distance, too. The region



defined by the vermilion figure is dotted with opaque white. The oral tentacles and the rhinophores are opaque white above, and vermilion below. The branchial papillae are as a rule banded with opaque white below the vermilion cap. The liver diverticulum within the respective papillae is dark brown. The general integument of the body including the sole is colorless.

Variation of color patterns is not rare. In the Specimen no. 7 there is a row of vermilion figures in the mid-dorsal line between the rhinophores and the tail. Specimen no. 2, which is uniformly vermilion-tinted on the head, is entirely free from those vermilion figures which occur dorsally in the normal specimens.

Here should be mentioned that *Aeolidiella multicolor* Macnae, 1954 from False Bay, South Africa is closely related to *A. takanosimensis* in the ornate colors of the body, but the 2 are different slightly from each other in the composition of the first several branches of the left posterior liver on the right side (see also MARCUS & MARCUS, 1967: 117).

Internal Anatomy: The jaws and radula are characterized fundamentally as usual in the genus *Aeolidiella*. That is, the jaw-edge is smooth, and the teeth of the radula are arcuated with a median emargination. The radular formulae examined are from $12 \times 0.1.0$ to $20 \times 0.1.0$. Each tooth is provided with 15 to 20 pectinate denticles on either side of the median cusp. It appears a little strange that the figured tooth of *Aeolidiella takanosimensis* from Baja California del Sur (FERREIRA & BERTSCH, 1975: 329; fig. 19) is low and somewhat more widened than that discussed in this paper.

The branches of the liver system are defined to correspond to the rows of papillae on back margins. Then there are many (6 to 7 in Specimen no. 3) branches in the right liver (and the left partner). The first several (4 in Specimen no. 3) branches of the left posterior liver on the

(← adjacent column)

Figure 2

Aeolidiella takanosimensis Baba, 1930

Specimen no. 9, length 13 mm

Living animal from dorsal (A) and ventral (B) sides

a - genital orifices b - nephroproct c - anus

d - opaque white patches in the median dorsal line

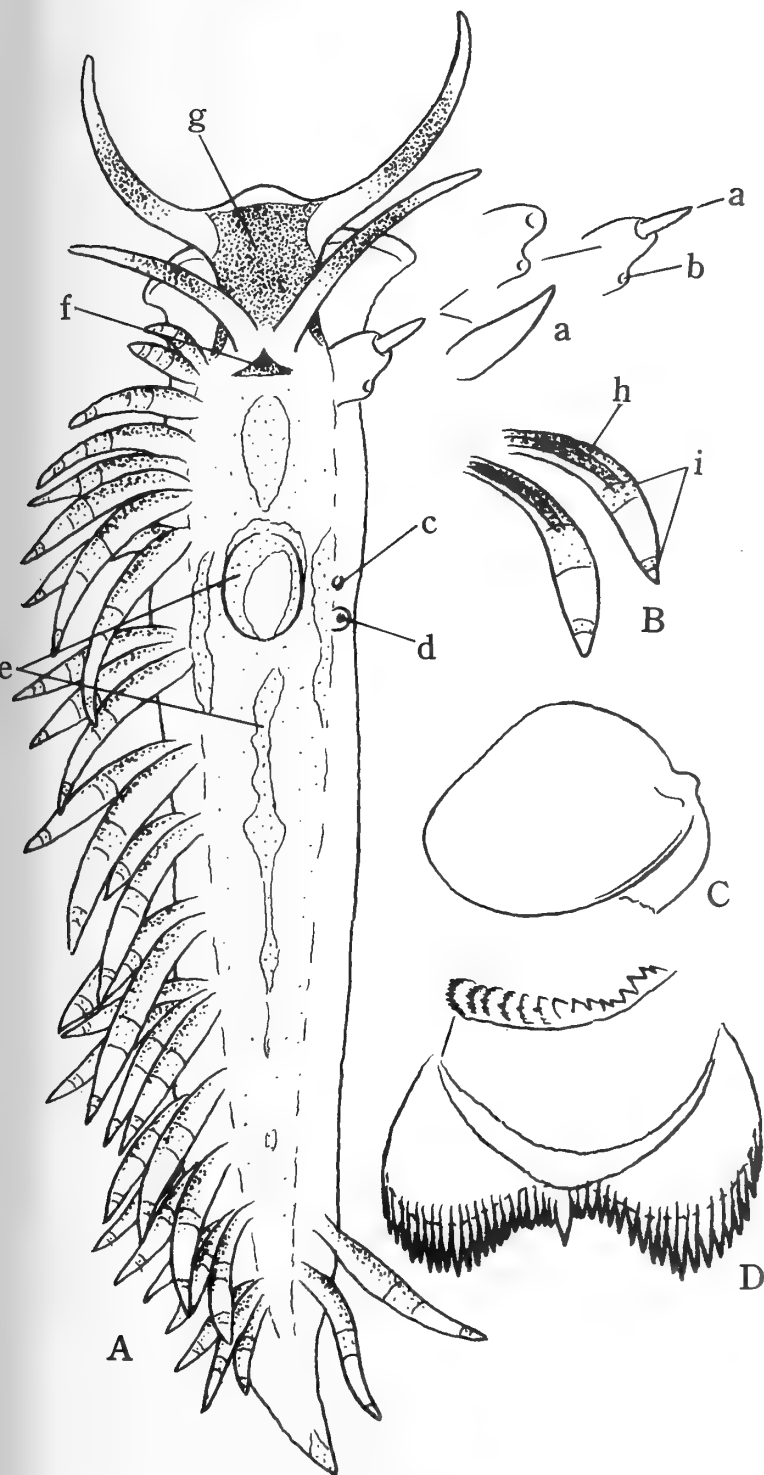
e - vermilion-tinted figure in the back

f - opaque white patch on the head

g - dark brown liver diverticulum

h - opaque white band

i - vermilion cap



right side are collected into a group within which is found a cleioproctus anus (the anus is sometimes pleuroproctus as described previously). In *Aeolidiella multicolor* the first several branches (in the present author's opinion) of the left posterior liver on the right side tend to form arches, and the anus opens behind the first one of these arches (see also MARCUS & MARCUS, 1967: 117).

The mouth part has 2 pairs of accessory glands: (1) The salivary glands are narrow band-like as usual. (2) The oral glands are each in the form of an elongated sac which debouches into the oral tube at about the opening of the pharynx. The duct of the sac is short, and the wall of the sac itself is accompanied by gigantic cells.

The genital complex could not be analyzed thoroughly. The penis is muscular, conical, and unarmed (see also SCHMEKEL, 1970: 155; fig. 16b). The vas deferens is prostatic throughout the length. A single spermatocyst is present.

Remarks: The genus *Aeolidiella* Bergh, 1867, together with the type species, *Eolida soemmerringii* Leuckart, 1828 (see SUTER, 1913: 581; LEMCHE, 1964: 118, 119) does not appear to be satisfactorily defined from the standpoint of taxonomy. Moreover, the morphology of *Eolida soemmerringii* remains mostly obscure (see TARDY, 1969: 34-35). But according to the suggestion by MACNAE, 1954: 36, the members of *Aeolidiella* may conveniently be divided into 2 groups (see also BURN, 1962: 126):

Group I: Species with the right liver many-branched.

Group II: Species with the right liver in the form of an arch.

At present it seems reasonable to classify *takanosimensis* Baba, 1930 within Group I of the genus *Aeolidiella* in the usual sense.

The following species from Japan are then referable to Group II:

(← adjacent column)

Figure 3

Aeolidiella takanosimensis Baba, 1930

Specimen no. 2, length 10 mm

A presumed variant in the coloration of the body

- A: living animal from dorsal side B: branchial papillae
C: right jaw ($\times 30$) D: tooth ($\times 240$)
a - protruded penis b - female orifice c - nephroproct
d - anus e - opaque white patches in the median dorsal line
f - vermillion bar behind the rhinophores
g - vermillion tinge on the head
h - vermillion tinge on the papillae i - opaque white bands

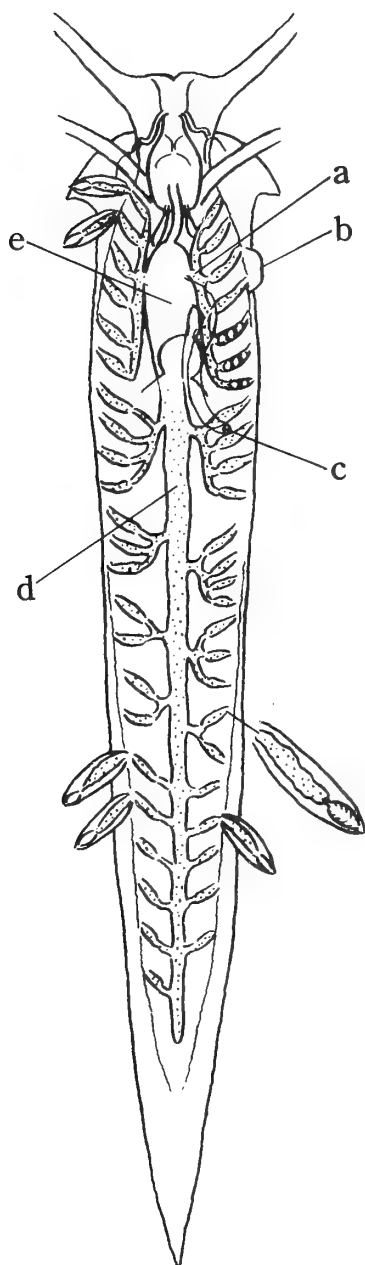


Figure 4

Aeolidiella takanosimensis Baba, 1930

Specimen no. 3, length 12 mm

Digestive system [mainly dissected by I. Hamatani]

a - right liver b - genital orifices c - anus
d - left posterior liver e - stomach

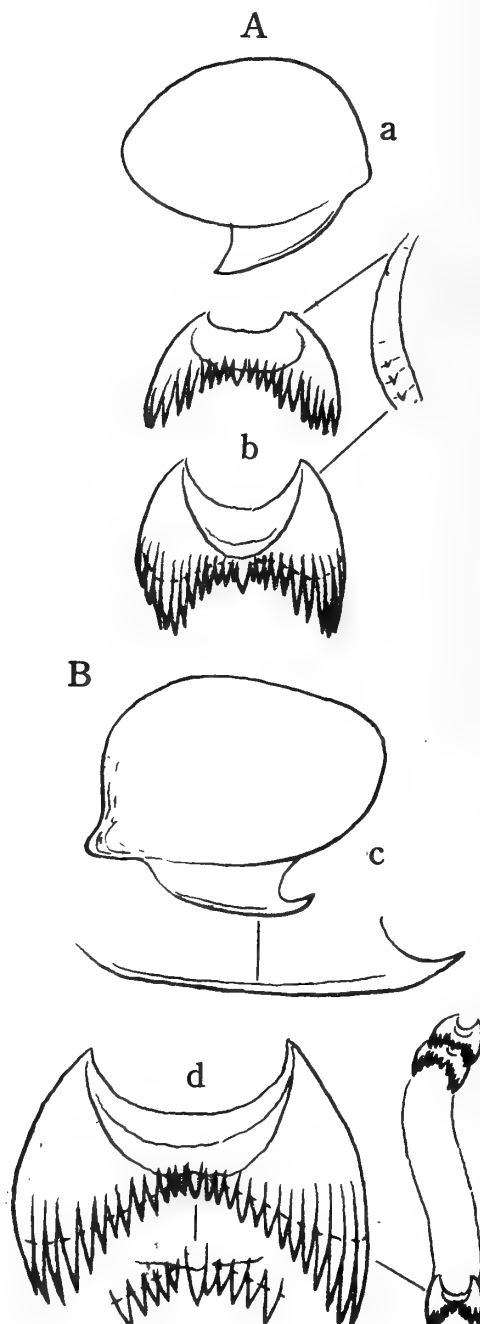


Figure 5

Aeolidiella takanosimensis Baba, 1930

A: Specimen no. 1, length 10 mm

a - right jaw ($\times 20$) b - teeth ($\times 110$)

B: Specimen no. 5, length 9 mm

c - left jaw ($\times 30$) d - tooth ($\times 150$)

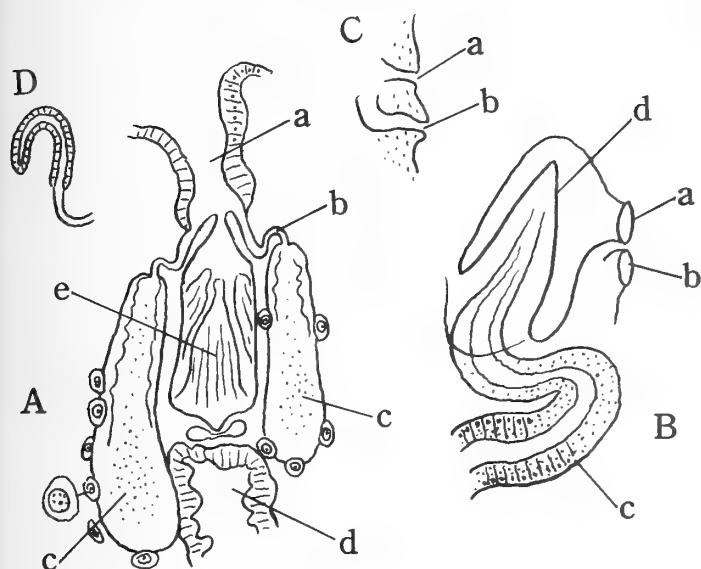


Figure 6

Aeolidiella takanosimensis Baba, 1930

A: Specimen no. 4, length 10 mm

Anterior part of the digestive system from dorsal side ($\times 30$)a - oral tube b - duct of the oral gland (c) d - stomach
e - pharynx

B: The same specimen

Anterior part of the reproductive system from dorsal side ($\times 80$)a - male orifice b - female orifice
c - prostatic vas deferens d - penis

C: Specimen no. 8, length 10 mm

Nephroproct (a) and anus (b) as seen from a horizontal section ($\times 20$)

D: The same specimen

Salivary gland ($\times 20$)1. *Aeolidiella japonica* Eliot, 1913

(Japanese name: Yamato-minoumiushi)

2. *Aeolidiella alba* Risbec, 1928

(Japanese name: Shiro-minoumiushi, new name; new record for Japan)

In these 2 species the anus is found far behind the first right arch of the left posterior liver (see also TARDY, 1969: 19; plt. 9). In the genera *Berghia* Trinchese, 1877 and *Spurilla* Bergh, 1864 the right liver is arched, and the anus lies within the first arch of the left posterior liver on the right side. *Berghia* is separated from *Spurilla* merely by having granulated rhinophores and produced foot corners (in *Spurilla* the rhinophores are perfoliated and the

foot corners are rounded). Two species of *Berghia* were previously recorded from Japan:

1. *Berghia japonica* (Baba, 1933)= *Baeolidia japonica* Baba, 1933

(Japanese name: Yamato-wagushi-minoumiushi)

2. *Berghia major* (Eliot, 1903)= *Baeolidia major amakusana* Baba, 1937

(Japanese name: Wagushi-minoumiushi)

SUMMARY

1. *Aeolidiella takanosimensis* Baba, 1930 is redescribed on the basis of specimens collected from various stations of southern Japan.

2. This species is easily recognizable by the possession of vermilion-tinted figures on the head and back, and examples of individual variation of these figures are considered.

3. In order to find proper characters of the species other than the body colors, jaws and radular teeth, some information in connection with the liver system and part of the genital system is given based on sections of the animal.

4. A brief mention is made of the taxonomic separation of *Aeolidiella* from the two allied genera, *Berghia* and *Spurilla*.

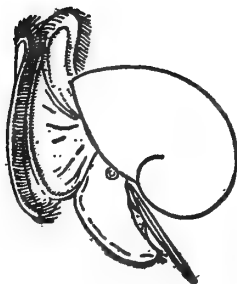
POSTSCRIPT

It was noticed that *Shinanoelolis* Baba, 1965 [type: *Cuthona* (*Hervia*) *emurai* Baba, 1937; Japanese name, Emura-minoumiushi] was synonymous with *Hermisenda* Bergh, 1878; furthermore, the species *emurai* was to be reidentified as *Hermisenda crassicornis* (Eschscholtz, 1831) from Alaska, Pacific North America and Mexico. According to MILLER, 1974, however, *Hermisenda* was referable to *Phidiana* Gray, 1850 (*s. l.*) (subfamily Facelininae in the meaning of MILLER, 1974).

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Anatomy, Ecology and Distribution of the Volutidae and Volutomitridae of the Southern Indian Ocean

(Gastropoda: Prosobranchia)

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(1 Plate; 10 Text figures)

THREE RECENT BENTHIC SURVEYS have been done with the M/S *Marion-Dufresne* in the subantarctic waters of the Indian Ocean. During cruise MD.03 (1974) several stations were made (including 50 macrobenthic samples) off Kerguelen, Heard and Crozet Islands between shallow water and 4200 m. Cruise MD.04 (1975) concentrated on the shelf around Kerguelen Islands, with 231 macrobenthic samples, and cruise MD.08 was mostly concerned with the Marion-Prince Edward shelf (49 macrobenthic samples) and the Crozet shelf (99 macrobenthic samples).

We collected 3 species of volutid and volutomitrid gastropods at 65 stations, in 73 samples, by trawls, dredges and grabs (Table 1): *Provocator pulcher* Watson, 1882; *Volutomitra curta* (Strebel, 1908) and *V. fragillima* Watson, 1882 (Figures 1 to 3). Study of the plentiful specimens provides the first thorough insight into these 2 allied neogastropod families in this area. Many faunistic and biogeographic data are recorded and the resulting distribution of the 3 species obtained is mapped (Figures 7, 8). Our anatomical studies, made with the help of D. van Weert, have led to discussion of several of their characteristics and assessment of their positions in the 2 families involved. The egg capsule of the volutid *Provocator pulcher* is also described and figured for the first time.

Family Volutidae

Provocator pulcher Watson, 1822

Provocator pulcher WATSON, 1882: 330, 331; 1886: 260, pl. 13, fig. 5; CARCELLES, 1947: 6; POWELL, 1960: 156; WEAVER & DUPONT, 1970: 123, fig. 53 F-G; CLOVER, 1975a: 10, 1 photo; 1975b: 1, 1 photo
Provocator provocator SOWERBY, 1887: 305, pl. 18, fig. 176; SMITH, 1942: 62, 63, pl. 13, fig. 95
Zidona (Provocator) pulchra WENZ, 1943: 1350, fig. 3822

Specimens (empty shells recorded in parentheses):

- Kerguelen Islands

MD.03: 7-CP4, 3; 11-CP7, (2); 13-CP9, 3; 17-CB5, 12 (3); 21-CP14, 5 (2); and 2 egg capsules (incl. 1 empty); 24-CB6, 5 (1)

MD.04: 7-CP13, 1 (2); 26-CP61, 2; 34-DC88, (1); 35-DC89, 1; 38-CP92, 1; 39-DC93, (1); 45-DR106, (2); 70-CP169, 1 egg capsule; 95-DC233, 1 egg capsule; 118-CP284, 1 (1)

- Crozet Islands

MD.08: 42-CP197, (1); 75-CP303, (3); 78-CP319, (2)

Distribution (Figures 7, 8):

The type locality is Kerguelen Islands, West Christmas Harbour, 48°43'S; 69°15'E, 105 fathoms [190 m], volcanic mud. Previously known only by empty shells (WATSON, 1882) and by shells from unknown stations off Kerguelen (CLOVER, 1975a, 1975b), the species is here re-

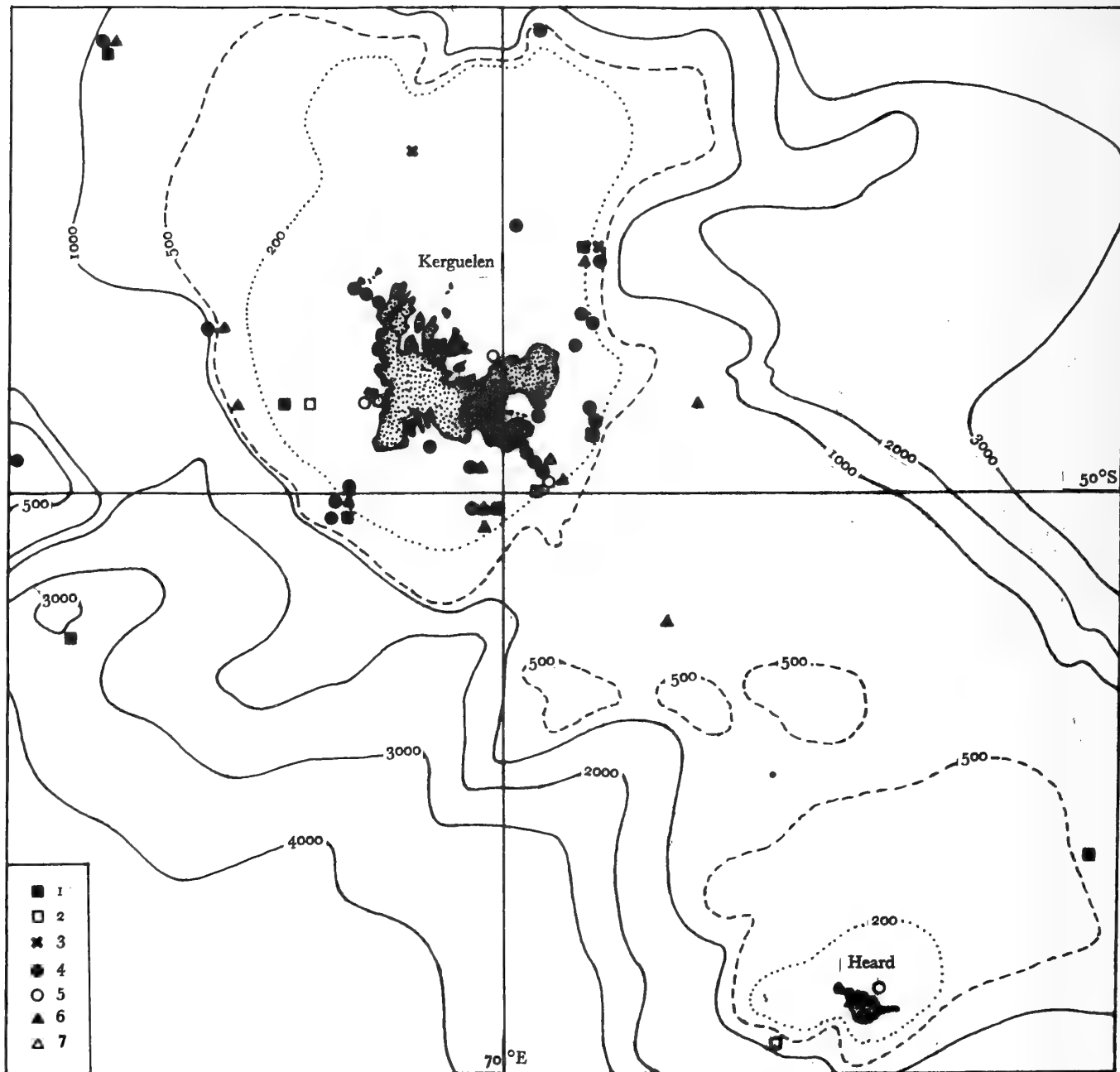


Figure 7

Present records of Volutidae and Volutomitridae off Kerguelen Islands and Heard Island: *Provocator pulcher* (1: living; 2: dead; 3: egg capsule), *Volutomitra fragillima* (4: living; 5: dead) and *Volutomitra curta* (6: living; 7: dead)

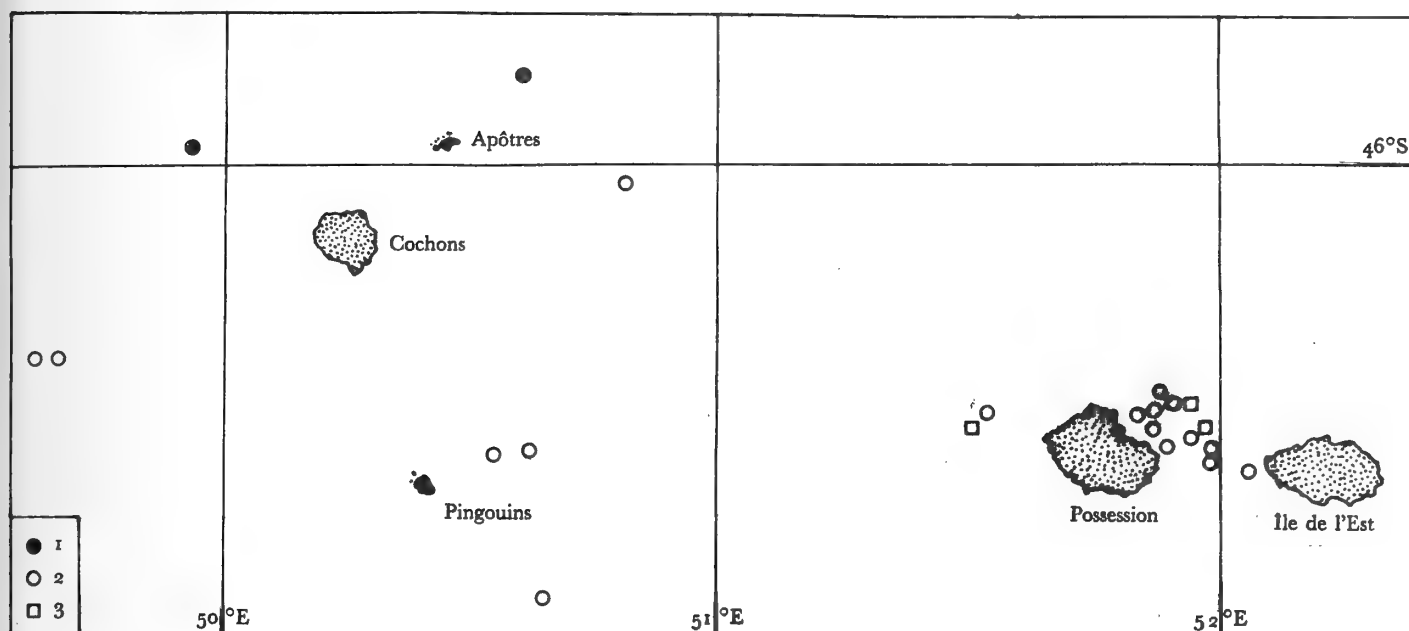


Figure 8

Present records of Volutidae and Volutomitridae around Crozet Islands: *Volutomitra fragillima* (1: living; 2 dead) and *Provocator pulcher* (3: dead)

corded living or dead from various stations on the Kerguelen - Heard plateau. For the first time it was also collected, but as dead material only, from the Crozet shelf: these empty shells may be remnants of a former extension of the distribution of this volute around Crozet Islands when the surrounding waters were colder than now. These records at Crozet are also interesting from the standpoint of their being from between *Provocator pulcher* of Kerguelen-Heard and *P. corderoi* Carcelles, 1947 (the only other known representative of the genus) from eastern South America.

Bathymetric Range: The bathymetric range for living specimens, as judged from the present records, is remarkably large: 155 to 3240 m! The apparent endemism of the species on the Kerguelen-Heard plateau is not easy to explain.

Ecology: Living on sandy to muddy substrates heavily mixed with blocks or gravels of basalt or pumice, a habitat which may explain the relative scarcity of this volute in

bottom samples taken in such adverse conditions.

Anatomy (Figures 9, 10): The maximum shell size observed in the present material and known for the species is 100.05 mm (total height). Animal of a rather uniform salmon pink coloration; foot anteriorly truncate, wide and flattened (Figure 9). Head laterally expanded; tentacles cylindric. Eyes on the anterior edge of lateral flat lobes of the head, just behind the tentacles (Figure 10). The siphon bears 2 equal lobes at its base; they are quite variable, sometimes as long as the siphon itself. Operculum absent. The mantle cavity has no unusual features worthy of description. It contains, from left to right, a bipectinate osphradium behind the siphon, a monopectinate ctenidium, the hypobranchial gland, the rectum and the anus, the renal pore and the genital duct.

The Alimentary Canal (Figure 11): The pleurembolic proboscis consists of a voluminous mass which is completely concealed in the proboscis sheath at rest. The retraction of the proboscis with its associated structures, odonto-

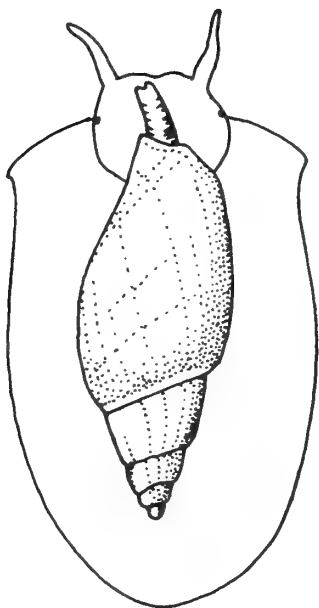


Figure 9

Provocator pulcher, in vivo

the dissected specimens, the wall of the mouth was highly plicated; it thus appears that the proboscis is capable of great dilation and elongation, permitting the ingestion of large prey.

The common duct of the paired accessory salivary glands opens just at the entrance of the mouth. The salivary ducts separately join the buccal cavity on its lateral sides just in front of its junction with the oesophagus. The odontophore opening into the buccal cavity is quite broad. The radular teeth are disposed in a single row. They are tricuspid, the median cusp being slightly longer than the laterals (Figure 12A). The 2 cartilages are situated on the sides of the radular ribbon.

As in most Muricacea, the oesophagus is composed of 3 distinct parts. The anterior oesophagus merges at the posterior end of the buccal mass. It is relatively long and terminates at the valve of Leiblein which begins the mid-oesophagus. It is a narrow tube approximately 1 mm wide. The muscular wall consists of an inner longitudinal and an outer circular layer. There are longitudinal ridges on its dorsal part. The lumen is lined with a cuboidal ciliated epithelium on most of its parts except a ventral area of much higher cells bordered with 2 prominent ridges. When moving toward the posterior end of the anterior oesophagus, this ventral area progressively sinks in the underlying tissues and forms a ventral groove. This groove

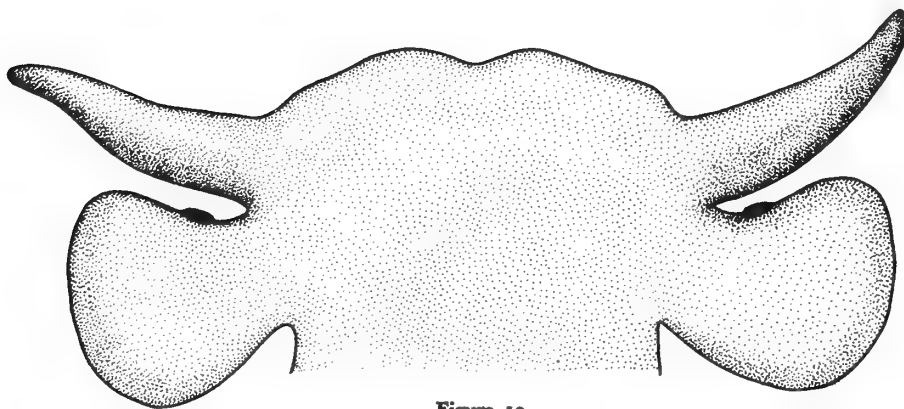


Figure 10

Provocator pulcher: dorsal aspect of the head

phore and the 2 pairs of salivary glands, pulls the oesophagus on the right side of the haemocoel. The buccal cavity communicates dorsally with the oesophagus, the odontophore lying ventrally. The floor is protected by a chitinous shield beginning just behind the oral cavity and extending close to the junction of the odontophore. In

can be clearly seen externally as a dark line on the underside of this part of the duct. There are a few scattered goblet cells.

The salivary ducts are buried in the muscular sheet of the oesophagus which they enter in front of the valve of Leiblein. Their free portions are relatively short. The

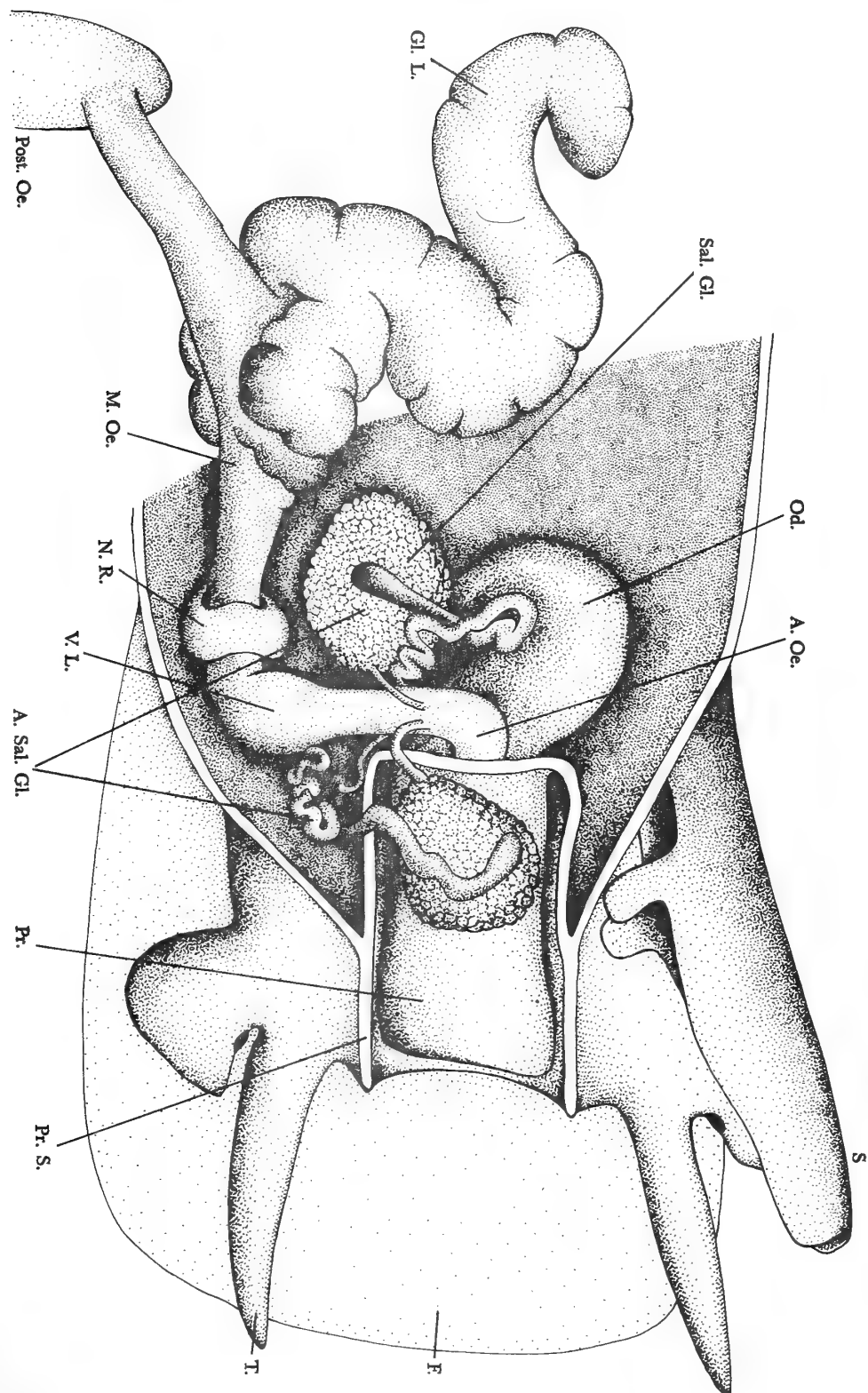
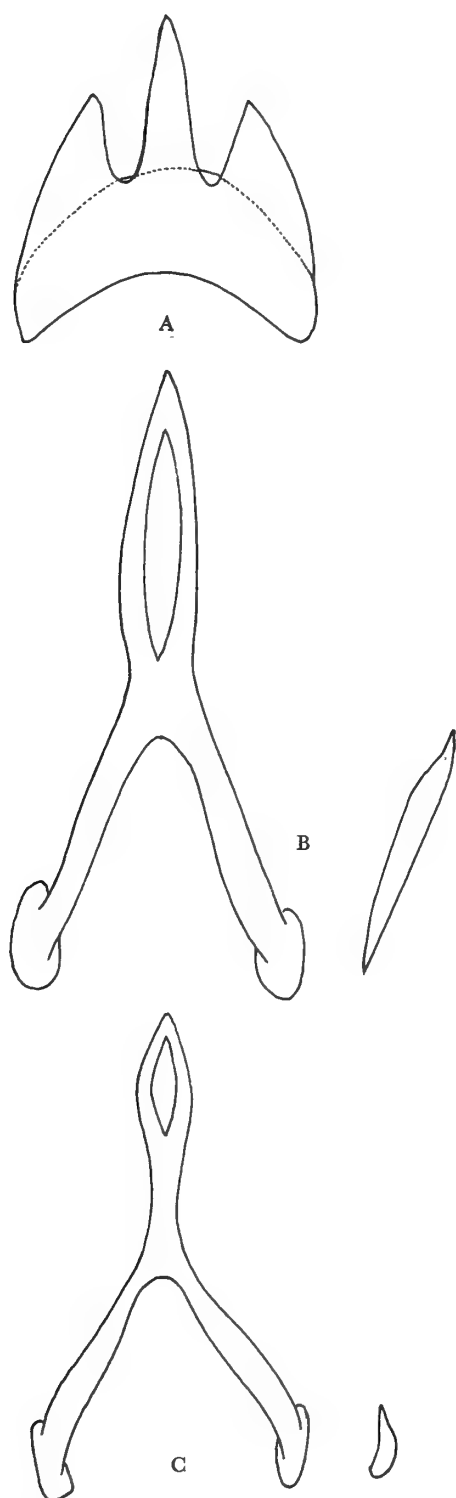


Figure 11

Provocator pulcher: anterior part of the digestive tract.

A. Oe. - anterior oesophagus A. Sal. Gl. - accessory salivary glands
 F - anterior part of foot Gl. L. - gland of Leiblein
 M. Oe. - mid-oesophagus N. R. - nerve ring
 Od. - odontophore Post. Oe. - post-oesophagus Pr. - proboscis
 Pr. S. - proboscis sheet Sal. Gl. - salivary glands
 S - siphon T - tentacle V. L. - valve of Leiblein



glands are compact and lie on both sides of the anterior oesophagus. Each gland consists of closely packed narrow tubules which are made of gland cells containing masses of granules and scattered ciliated cells. The collecting tubules and the salivary ducts are lined with a ciliated, cuboidal epithelium.

The accessory salivary glands are made of 2 long cylindrical processes loosely coiled around the salivary glands. They are about 0.8 mm in diameter. Each gland consists of an inner layer of non-ciliated epithelium. The outer layer is composed of circular muscle fibers surrounded by a composite tissue of gland cells, 2 or 3 thick cells, intermingled with circular and longitudinal muscle fibers. Excretory processes of the gland cells reach the central lumen individually. The accessory salivary ducts progressively lose the gland cells and become narrower. They join together below the odontophore in a very narrow tube, and open at the mouth.

The valve of Leiblein is a rather large bulb. It contains a conical prolongation of the anterior oesophagus into the middle oesophagus (Figure 13). The origin of this projecting rim is clearly demonstrated by its cellular organisation. Its internal wall is lined with an epithelium typical of the anterior oesophagus; ciliated cells, scattered mucocytes and many gland cells containing masses of red-stained granules. The outer wall of the cone is coated with an epithelium of green-stained mucocytes and ciliated cells. The outer wall of the bulb is lined with tall mucous cells with a basal nucleus, and ciliated supporting cells with a median nucleus. The non-ciliated groove of the anterior oesophagus remains as a ventral slit at the anterior part of the valve. It then turns progressively to the right and becomes dorsal at the posterior part of the valve. This feature reflects the torsion of the visceral mass. Immediately behind the valve, the mid-oesophagus suddenly narrows and passes through the nerve ring. The cellular composition of the mid-oesophagus changes abruptly. Histologically, the valve of Leiblein constitutes thus a clearcut limit between 2 distinct segments of the oesophagus. It is a characteristic feature of the *Rachiglossa*. Its main function "is probably to retain the enzymatic secretion from the unpaired foregut gland and from the glandular dorsal folds within the mid and posterior oesophagus" (PONDER, 1974: 313).

(← adjacent column)

Figure 12

Radular teeth of: A, *Provocator pulcher*; B, *Volutomitra fragilima*; C, *Volutomitra curta*

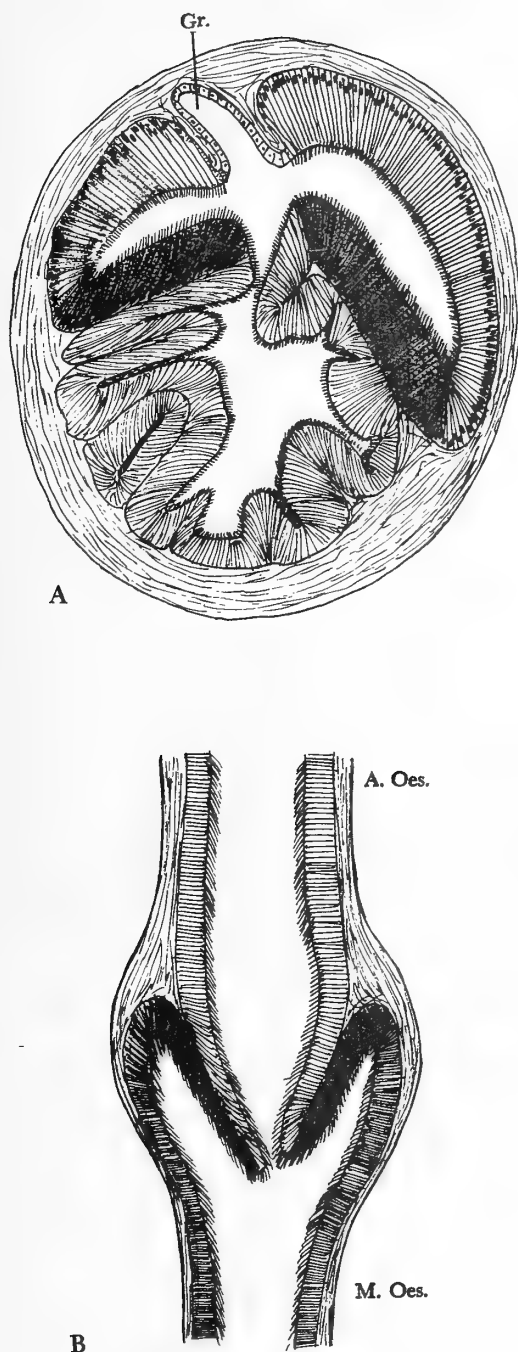


Figure 13

Provocator pulcher: valve of Leiblein; A, frontal section; B, transversal section. A. Oes. - anterior oesophagus. Gr. - non-ciliated groove. M. Oes. - mid-oesophagus.

When crossing the nerve ring, the mid-oesophagus has a diameter of about 1.5 mm. Its walls are thin. The muscular layer is very weak at its beginning, the fibers have the same disposition as in the anterior part. The external layer of circular muscle fibers is thicker. The inner epithelium forms a few low ridges. At a short distance from the beginning, the gland of Leiblein (Figure 11) begins with swellings that appear on the dorsal wall of the oesophagus. The gland is progressively differentiated as a tubular, elongate organ coiled upon itself in a compact mass surrounding the oesophagus. The lumen is alveolar with muscular compartments. The gland is composed of 3 distinct parts. The first is lined with tall columnar gland cells with few mucocytes; the muscular layer is very thin. In the next part, the wall has a thick muscular layer and bears longitudinal and transverse ridges. The glandular epithelium is composed of a higher percentage of mucocytes. The dead end of the gland forms a sac 2 to 2.5 mm wide. Its wall is very thin and lined in most of its parts by a flattened epithelium. There are a few scattered low ridges of gland cells comprising some mucocytes. The bad fixation of the tissues in this part of the digestive tract prevented better interpretation.

Unidentified food remnants have been found in this part of the alimentary canal. Behind the gland of Leiblein, the posterior part of the mid-oesophagus has a diameter of 1.9 mm; its internal wall bears many longitudinal ridges.

The posterior oesophagus is separated from the preceding part by a constriction. Its section increases rapidly to a diameter of 2 to 2.5 mm. The muscular layer is very thin, the epithelium consists of ciliated cells and mucocytes. There are digitated internal ridges.

The U-shaped stomach is a very simple sac with an internally plicated wall. The ridges of the dorsal part of the posterior oesophagus reach the single digestive gland aperture. The ventral ridges continue in the intestine without interruption.

The intestine runs from the stomach along the right pallial wall. Its diameter is 2 to 3 mm. The thin muscular layer is lined with an epithelium which is thickened into longitudinal ridges of columnar, ciliated gland cells with numerous dark granules. The mucocytes, scattered at the beginning, are much more abundant towards the end. The anal gland is a branching tubule derived from an invagination of the renal wall. Its cells are ciliated and granular.

Discussion: With these observations, it is possible to determine the systematic position of the genus *Provocator*. This genus has been classified in the subfamily Zidoninae by CLENCH & TURNER (1964) on the basis of the morpho-

logy of the radula. This placement is corroborated by the following observations:

- uniseriate radula with tricuspid teeth;
- accessory salivary glands loosely bound around moderately compact salivary glands;
- lobes at the bases of the siphon of equal development;
- absence of operculum.

It should be added that the genus *Provocator* could be considered more primitive than *Alcithoe* by the fact that its gland of Leiblein is less detached from the oesophageal wall than in the latter genus (compare the anatomical description of *Alcithoe arabica* by PONDER, 1971).

On the specific level, the very close similarity should be noted between the radular teeth of *Provocator pulcher* (Figure 12A) and *P. corderoi* (cf. pl. 107 in CLENCH & TURNER, 1964); the teeth of the latter species are somewhat more slender, with more arcuate bases.

Family Volutomitridae

Volutomitra curta (Strebel, 1908)

Paradmete curta STREBEL, 1908: 23, pl. 3, figs. 34a-e; POWELL, 1951: 166; CARCELLES, 1953: 196; POWELL, 1958: 198; 1960: 157

Paradmete longicauda STREBEL, 1908: 24, pl. 3, figs. 36a-b; POWELL, 1951: 165; CARCELLES, 1953: 196, pl. 3, fig. 70

Volutomitra (Paradmete) curta. CERNOHORSKY, 1970: 103, pl. 13, figs. 11-13

Specimens (all from Kerguelen Islands):

MD.03: 3-CP2, 6 (1); 3-DS1, 1; 6-CP3, 3; 17-CB5, 70 (9); 21-CP14, 1; 24-CB6, 2

MD.04: 15-DC37, 1; 17-DC39, 1; 24-DR58, 1 (2); 38-CP92, 1; 47-DC108, 1; 82-CP196, (1); 113-DC269, (1); 115-DC275, 1

Distribution: The type locality is Shag Rock Bank, 53° 34'S, 43° 23'W, 160 m, gravel and sand, bottom temperature +2.05°C. It was known from Shag Rock Bank,

South Georgia Island, Enderby Land, Mackenzie Sea. First recorded here (cf. Figure 7) from Kerguelen Islands, a major northward extension of range of this volutomitrid. Not obtained at Crozet Islands or Marion/Prince Edward Islands during our surveys.

Bathymetric Range: Was known living from 75 to 300 m. Thus it is of interest to point out that this species was obtained living off Kerguelen Islands from 120 m to as deep as 650 m (present material).

Ecology: Rather similar to that of *Volutomitra fragillima* (the 2 species are frequently collected together) but with a lower temperature-tolerance which would account for its absence from both the Crozet and Marion/Prince Edward shelves.

Anatomy (Figures 14, 15): Animal rather small; maximum height of the shell: 28.6 mm. Tentacles cylindrical, bearing eyes on their posterior side. Operculum present.

The Alimentary Canal:

The pleurembolic proboscis is relatively long. The wall of the proboscis sheet is transversely plicate. The strong retractor muscles connect its sides to the lateral walls of the body. The ventral wall of the buccal cavity is protected by a chitinous shield. The accessory salivary gland is an unpaired organ as in other Volutomitridae. This gland is quite small and entirely concealed in the proboscis. Its thin secretory duct lies just behind the chitinous shield of the buccal floor and opens at the mouth aperture. Histologically the gland consists of a tube lined with cubic epithelium, the cells possessing large nuclei, and an outer layer of circular muscle fibers. Few gland cells are situated in its terminal part. The radula is triseriate. The central tooth is quite large with a single thin lanceolate cusp and 2 long basal processes (Figure 12C). The lateral teeth are small and short.

The salivary glands are small; the secretory tubules are composed of one type of cell. The salivary ducts enter the wall of the oesophagus in front of the valve of Leiblein. They open into the buccal cavity close to the junction of

Explanation of Figures 1 to 6

Figure 1: *Provocator pulcher*, height 85 mm, from Kerguelen Islands, MD. 03-24-CB6

Figure 2: *Volutomitra curta*, height 15.6 mm, from Kerguelen Islands, MD. 03-17-CB5

Figure 3: *Volutomitra fragillima*, height 15.4 mm, from Kerguelen Islands, MD. 04-F51-DC119

Figure 4: Egg capsule of *Provocator pulcher* on a valve of *Malletia gigantea* measuring 47 × 28 mm; Kerguelen Islands, MD 04-H95-DC233

Figure 5: Two egg capsules of *Provocator pulcher* on an egg capsule of skate, Kerguelen Islands, MD. 03-21-CP14

Figure 6: The same capsules, enlarged



Figure 1

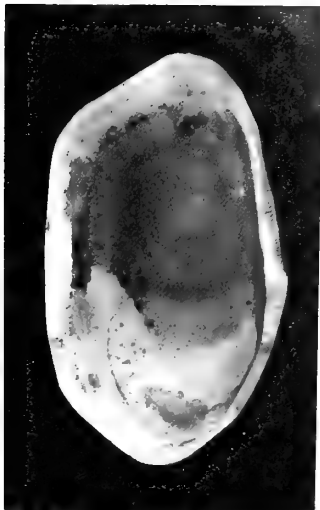


Figure 4



Figure 2

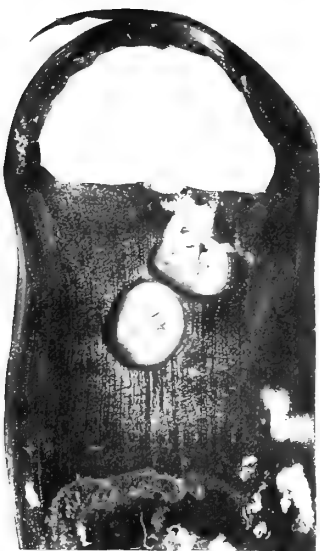


Figure 5

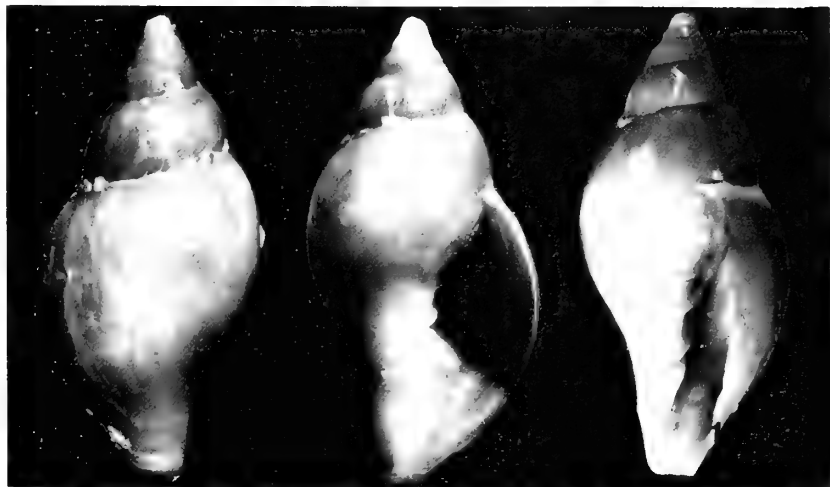


Figure 3



Figure 6

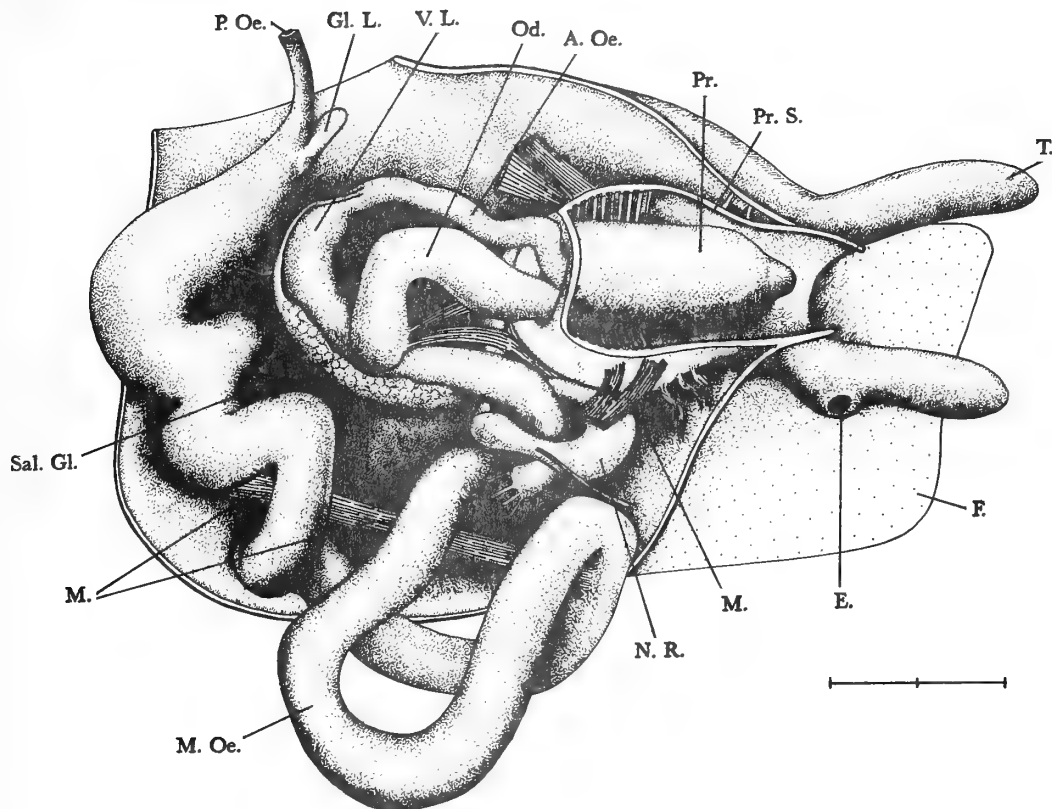


Figure 14

Volutomitra curta: anterior part of the digestive tract. Abbreviations as for Figure 11. E - eye M - muscular bundles

the oesophagus. The ducts are densely ciliated, the cilia having a forward orientation.

The anterior oesophagus is relatively narrow. There are 2 lateral ciliated ridges. Ventrally the epithelium is composed of flattened, nonciliated cells. Gland cells filled with red granules are in all this part of the digestive tract.

The mid-oesophagus begins with the valve of Leiblein. The tract is rather long and coiled upon itself, a strong muscular bundle is attached between 2 loops. The valve of Leiblein, situated well in front of the nerve ring, is quite typical. The ventral non-ciliated groove of the anterior oesophagus persists as a deep slit into the fold of the valve. This groove, ventral in the anterior part of the valve, moves progressively to the right and becomes dor-

sal posteriorly. This evidence of torsion thus occupies the same level as in the Volutidae. Two bundles of longitudinal muscle fibers are developed into the wall of the valve, below the ridges lining the non-ciliated groove. The histological organisation of the valve corresponds to the one observed in *Provocator*, except the 2 conspicuous muscular bundles present in its walls. The mid-oesophagus possesses a ciliated groove which corresponds to the pretorsional dorsal alimentary tract of the anterior oesophagus. At its beginning, the wall of the mid-oesophagus is thin; later on, it becomes thicker by increase of the internal layer of circular muscle fibers. The numerous mucocytes and the red-stained cells that constitute the dorsal epithelium of the first part of the mid-oesophagus are pro-

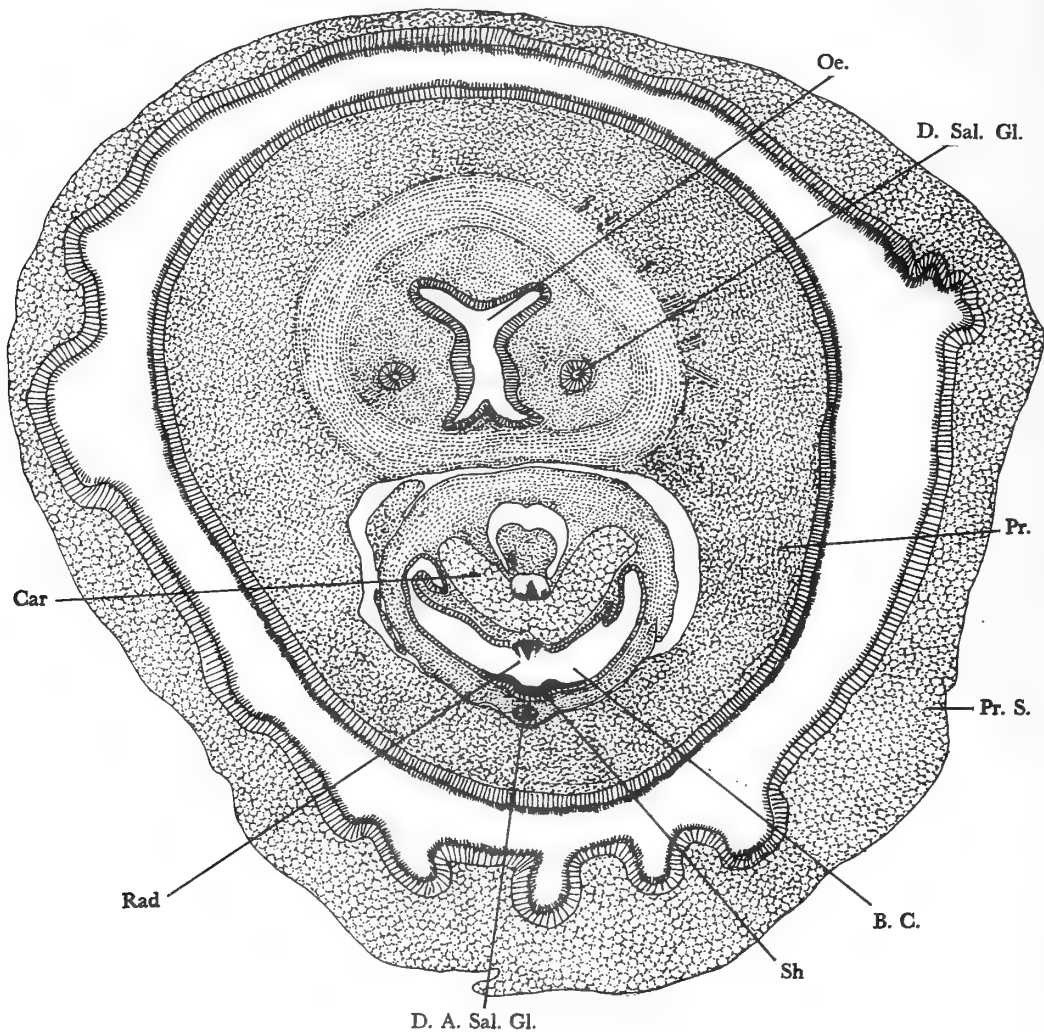


Figure 15

Volutomitra curta: transverse section through proboscis.

B. C. - buccal cavity Car. - subradular cartilage D. A. Sal. Gl. - common duct of accessory salivary glands Rad. - radula
Oe. - oesophagus Pr. - proboscis Pr. S. - proboscis sheet

gressively replaced by gland cells of irregular shape and filled with brown granules. These latter elements are restricted to the dorsal part of the lumen and are separated from the ventral ciliated groove by 2 low ciliated ridges. Further on the dorsal part is completely isolated and forms the gland of Leiblein. At its posterior end, the gland emerges out of the wall of the mid-oesophagus as a small

translucent vesicle. Its histology seems to be uniform.

The transition from the mid-oesophagus to the posterior oesophagus is visible externally as a rapid decrease in the external diameter of the duct. Nevertheless, the size of the lumen remains constant, as there is a considerable diminution of the muscular layers of the wall. The lumen is lined with ciliated epithelium.

Volutomitra fragillima (Watson, 1882)

Voluta fragillima WATSON, 1882: 334; 1886: 263, pl. 14, fig. 7; THIELE, 1912: 248; LAMY, 1915: 69; SMITH, 1915: 74

Paradmete typica STREBEL, 1908: 22, pl. 3, figs. 35a-35f; MELVILL & STANDEN, 1912a: 357; 1912b: 131; THIELE, 1912: 248, fig. 12 (radula)

Paradmete fragillima. CARCELLES & WILLIAMSON, 1951: 303; POWELL, 1951: 165; CARCELLES, 1953: 196; POWELL, 1957: 134; 1958: 199; 1960: 157

Volutomitra (Paradmete) fragillima. CERNOHORSKY, 1970: 102, figs. 186-187 (radula), 190-191 (protoconch), pl. 13, fig. 10

Specimens:

- Kerguelen and Heard Islands

"*La Japonaise*" 1974: SMK324, (1)

MD.03: 2-DC1, 2 (1); 2-CB2, 1; 14-CB3, 1; 17-CB5, 33, (2); 21-CP14, 2; 22-CP15, 2; 24-CB6, 8 (1); 25-CB7, 2 (2)

MD.04: 2-DC4, 1 (1); 4-DC7, 1; 5-DC8, 5; 10-DC20, (2); 15-DC37, 1; 21-DC54, 1; 24-DR58, 1 (2); 26-CB60, 2; 31-DC82, (1); 47-DC108, 1; 50-DC117, 1 (5); 51-DC119, 1; 54-BB127, (1); 59-DC140, 5 (3); 79-DC189, 1; 84-DC200, (2); 90-DC128, 1; 96-CP237, 1; 102-DC252, 4 (1); 108-CP261, 3; 112-DC268, 1; 114-DC272, 2 (27); 115-DC275, (1)

- Crozet Islands

MD.03: 26-CP17, (1); 30-CP21, (1)

MD.08: 9-CP64, (3); 9-CP66, (1); 9-DC68, 2 (23); 9-CP74, 1 (12); 9-CP75, (3); 40-DC186, (76); 50-DC216, 1 (1); 59-DC252, 1 (1); 67-DC271, (2); 68-CP275, (2); 71-DC283, (1); 72-DC289, (1); 73-CP295, (2); 75-CP303, (1); 76-DC309, (1); 77-DC314, (28); 78-CP319, (1); 79-DC322, (1)

Distribution (Figures 7, 8):

Type Locality: Royal Sound, Kerguelen Islands, 49°28'S, 70°13'E, 28 fathoms [51 m] (*Volutomitra fragillima*); South Georgia, Cumberland Bay, 54°17'S, 36°28'W, 75 m (*Paradmete typica*). Was known from Burdwood Bank, South Georgia Island, Palmer Archipelago, Enderby Land, Kemp Land, Kaiser Wilhelm Land, Oates Land, and Kerguelen Islands. First recorded here as living around Crozet Islands and as dead off Heard Island. It seems to be absent from the Marion shelf, and is mostly observed as empty shells around Crozet Islands, where it probably flourished some time in the past.

Bathymetric Range: Was known from 30 to 603 m. We obtained it living in 37 - 585 m at Kerguelen Islands and in 150 - 210 m at Crozet Islands.

Ecology: This species seems to be eurytopic as far as the nature of the substrate is concerned, but it is particularly abundant on muddy substrates mixed with biogenic fragments (bryozoans, shells, foraminiferans, etc.). Its relative rarity alive around Crozet Islands (5 living out of 146 specimens, as compared with 84 living out of 136 specimens from around Kerguelen-Heard) suggests its recent regression there; a slight rise in water temperature could have caused this.

Anatomy: The animal is very similar to that of *Volutomitra curta* except that the operculum is absent. Maximum height of the shell: 23.0 mm.

The Alimentary Canal:

The pleurembolic proboscis is developed as in the first species. The upper part of the mouth bears a V-shaped jaw. The floor of the buccal cavity bears also a chitinous plate, but much bigger and more depressed than in the first species. The accessory salivary gland is more developed but still completely concealed in the proboscis. It is composed of an inner cubic epithelium, an intermediate layer of circular muscle fibers, and external gland cells (Figure 12B). The radula is triseriate, the median tooth (Figure 12B) is Y-shaped, the 2 laterals are needle-like and more developed than in *Volutomitra curta*. The organisation of the anterior oesophagus and the salivary glands are nearly identical in both volutomitrids.

The valve of Leiblein is quite different structurally and seems to correspond to a more primitive state. The projecting ring is absent functionally and replaced by the very long cilia directed backwards. The glandular organisation is very similar in both species. The non-ciliated groove cuts very deeply into the ventral wall of the duct. The 2 longitudinal muscles in the wall behind the edges of the groove are also present.

Besides the differences observed in the structure of the valve of Leiblein, the mid-oesophagus shows great similarities. It should be noted that the dorsal tract of gland cells characteristic of the gland of Leiblein is more characterized.

Discussion: Our observations can be added to the relatively few data available on the anatomy of the Volutomitridae (see PONDER, 1972, 1974). The characters of the radula correspond well with the published observations. An unpaired accessory salivary gland is shared with the other Volutomitridae and the Marginellidae. In the 2 species studied here this gland is completely embedded in the proboscis.

In both species the region of torsion is situated in the area of the valve of Leiblein. This position is different

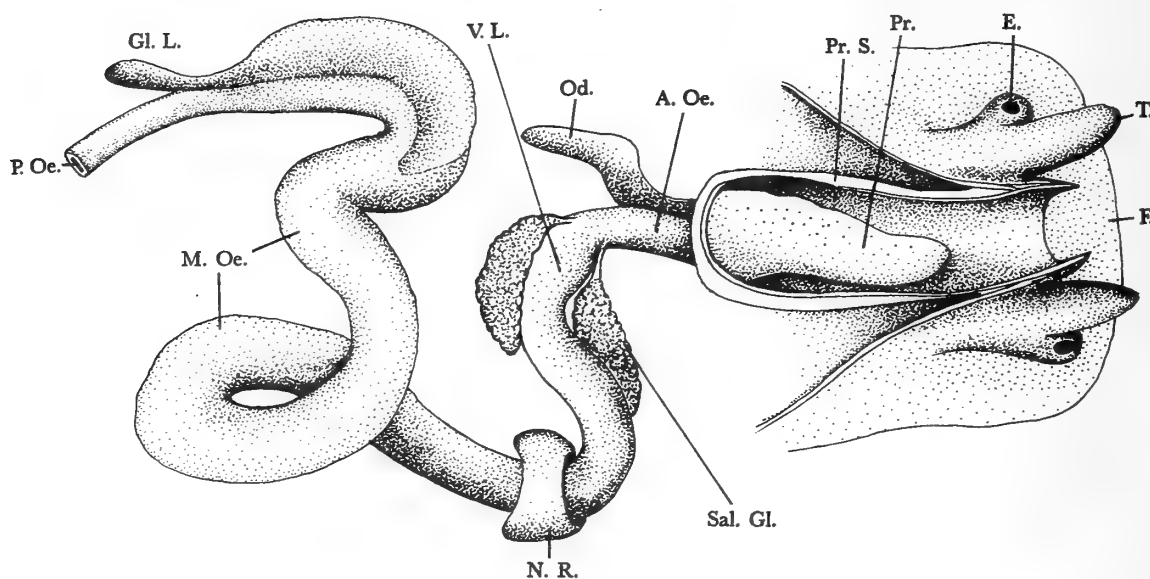


Figure 16

Volutomitra fragillima: anterior part of the digestive tract. Abbreviations as for Figure 11

from what has been found in other species where it is situated behind the valve (PONDER, 1972). There is an important difference in the stage of development of the valve of Leiblein besides a similar glandular equipment in both species. In *Volutomitra fragillima*, the valve is built up of long cilia only, and there is no projecting rim. Our observations on the organization of the gland of Leiblein corroborate PONDER's (1974) hypothesis on the forwards formation of the gland of Leiblein from the dorsal part of the oesophagus.

The differences observed between the 2 species studied here should be pointed out:

	<i>Volutomitra</i>	
	<i>curta</i>	<i>fragillima</i>
operculum	absent	present
radula: lateral teeth	reduced	needle-like
valve of Leiblein	with a projecting rim	long cilia, no rim

It seems thus that the 2 species should be classified in 2 supraspecific taxa. Present knowledge of other species of Volutomitridae does not permit us to place the species in already described taxa or to create a new one.

Provocator pulcher EGG CAPSULES

We got the previously unknown egg capsules of *Provocator pulcher* at 3 stations in the North of the Kerguelen Islands: MD.03-21/CP14 (360 - 345 m) and MD.04-70/CP169 (104 m) and MD.04-95/DC233 (195 m). These capsules are almost hemispherical, 17 - 18 mm in diameter and 7 - 8 mm high. This shape is the common one among the Volutidae, and has recently been described (ARNAUD, 1978) in *Harpovoluta charcoti* Lamy, the southernmost volutid, living in true Antarctic waters. Free subspherical capsules are well known (cf. for example ORBIGNY, 1842) in the magellanic volutid *Adelomelon brasiliensis* (Lamarck, 1814).

The capsules of *Provocator pulcher* are very similar in the 3 samples mentioned. In sample 21/CP14, one empty capsule and another one containing 4 young (Figures 5, 6) are firmly fixed on the surface of a large living egg capsule of a skate (112 × 71 mm excluding the 4 terminal processes). In the sample 70/CP169, a capsule again with 4 young was detached during trawling from an egg capsule of another skate (the corrugations of which are obvious on the basal surface of the volutid egg capsule).

Thus in both samples, from depths between 204 and 345 m, these egg capsules of *Provocator pulcher* have sim-

Table 1

Data of M/S "Marion-Dufresne" stations where Volutidae and Volutomitridae were collected during cruises MD.03, MD.04 and MD.08.

Cruise	Station	Sample ¹	S. Lat.	E. Long.	Area	Date	Depth (m)
MD.03 (1974)	2	DC1	49°30.7	70°44.7	E. Kerguelen	4.4	115
	2	CB2	49°33.2	70°47.1	E. Kerguelen	4.4	130
	3	CP2	49°25.4	71°51.7	E. Kerguelen	4.5	650-620
	3	DS1	49°28.5	71°51.8	E. Kerguelen	4.5	650
	6	CP3	50°37.9	71°35.8	SE Kerguelen	4.6	565
	7	CP4	52°12.7	75°38.4	NE. Heard	4.7	560-520
	8	DC6	52°59.4	73°38.0	N. Heard	4.8	90
	11	CP7	53°20.3	72°29.2	W. Heard	4.9	790
	13	CP9	50°49.1	65°39.9	SW. Kerguelen	4.12	3240
	14	CB3	49°45.8	64°50.6	W. Kerguelen	4.13	262
	17	CB5	47°24.9	66°04.0	NW. Kerguelen	4.14	585
	21	CP14	48°29.7	70°55.4	NE Kerguelen	4.15	360-345
	22	CP15	48°58.5	70°51.1	NE. Kerguelen	4.16	105-90
	24	CB6	50°10.7	69°48.7	SE. Kerguelen	4.17	195
	25	CB7	50°01.7	68°27.3	SE. Kerguelen	4.17	172
	26	CP17	46°24.0	51°59.0	Crozet	4.20	180
	30	CP21	46°02.3	50°50.2	Crozet	4.22	187
MD.04 (1975)	2	DC4	49°29.3	70°22.2	E. Kerguelen	2.22	44
	4	DC7	49°29.8	70°40.5	E. Kerguelen	2.22	96
	5	DC8	49°30.6	70°54.5	E. Kerguelen	2.22	140
	7	CP13	49°32.1	70°57.0	E. Kerguelen	2.22	149-155
	10	DC20	49°33.2	69°40.8	S. Kerguelen	2.23	49-53
	15	DC37	49°54.8	69°47.2	SE. Kerguelen	2.23	120
	17	DC39	50°11.1	69°53.0	SE. Kerguelen	2.24	263-252
	21	DC54	49°41.4	69°18.3	S. Kerguelen	2.24	110
	24	DR58	50°04.0	68°29.0	SW. Kerguelen	2.25	195
	26	CB60	50°03.4	68°28.3	SW. Kerguelen	2.25	192-198
	26	CP61	50°05.8	68°25.0	SW. Kerguelen	2.25	207
	31	DC82	49°27.4	68°46.8	W. Kerguelen	2.26	63
	34	DC88	49°27.4	68°10.7	W. Kerguelen	2.27	185
	35	DC89	49°28.0	67°53.1	W. Kerguelen	2.27	191
	38	CP92	49°29.0	67°24.2	W. Kerguelen	2.27	249
	39	DC93	49°08.7	68°54.0	W. Kerguelen	2.28	60
	45	DR106	49°00.3	67°30.4	W. Kerguelen	3.1	206
	47	DC108	48°59.1	67°07.9	W. Kerguelen	3.1	315
	50	DC117	48°47.1	68°49.3	NW. Kerguelen	3.2	70
	51	DC119	48°44.0	68°45.1	NW. Kerguelen	3.3	95
	54	BB126	48°19.0	67°56.5	NW. Kerguelen	3.3	188
	54	BB127	48°19.0	67°56.5	NW. Kerguelen	3.3	192
	59	DC140	48°41.4	68°38.6	NW. Kerguelen	3.4	104
	70	CP169	47°42.2	68°56.5	N. Kerguelen	3.7	204
	79	DC189	49°04.0	69°21.3	N. Kerguelen	3.8	37
	82	CP196	48°55.4	69°31.1	N. Kerguelen	3.8	209-305
	84	DC200	49°08.4	69°56.2	NE. Kerguelen	3.9	50
	90	DC218	48°19.3	70°09.0	NE. Kerguelen	3.10	128
	95	DC233	47°09.6	70°28.1	NE. Kerguelen	3.11	195
	96	CP237	47°07.5	70°28.8	NE. Kerguelen	3.11	201-204
	102	DC252	48°56.6	70°50.8	NE. Kerguelen	3.13	95
	108	CP261	49°03.4	70°41.3	NE. Kerguelen	3.14	76
	112	DC268	49°46.3	70°15.1	SE. Kerguelen	3.14	104
	113	DC269	49°50.2	70°21.2	SE. Kerguelen	3.15	147
	114	DC272	49°54.5	70°24.4	SE. Kerguelen	3.15	168
	115	DC275	49°58.0	70°29.1	SE. Kerguelen	3.15	234
	118	CP284	49°58.6	70°28.7	SE. Kerguelen	3.15	245-185

Table 1 (continued)

Cruise	Station	Sample ¹	S. Lat.	E. Long.	Area	Date	Depth (m)
MD.08 (1976)	9	CP64	46°10.8	51°49.6	Crozet	3.21	120-150
	9	CP66	46°23.1	51°52.8	Crozet	3.21	90-110
	9	DC68	46°22.9	51°51.2	Crozet	3.21	125
	9	CP74	46°22.4	51°54.3	Crozet	3.22	150-160
	9	CP75	46°19.8	51°52.3	Crozet	3.22	150-340
	40	DC186	46°21.1	51°33.9	Crozet	4.14	171
	42	CP197	46°21.4	51°34.9	Crozet	4.14	172-220
	50	DC216	45°51.5	50°37.8	Crozet	4.16	150
	59	DC252	45°59.9	49°59.3	Crozet	4.17	210-217
	67	DC271	46°16.8	49°37.4	Crozet	4.18	277-280
	68	CP275	46°16.6	49°37.0	Crozet	4.18	270-262
	71	DC283	46°37.5	50°39.0	Crozet	4.19	268-270
	72	DC289	46°23.4	50°32.0	Crozet	4.19	187-155
	73	CP295	46°24.3	50°37.8	Crozet	4.20	263-412
	75	CP303	46°19.9	51°52.9	Crozet	4.20	155-257
	76	DC309	46°26.0	52°03.6	Crozet	4.20	50
	77	DC314	46°25.0	51°59.7	Crozet	4.21	270-247
	78	CP319	46°23.7	51°58.1	Crozet	4.21	142-170
	79	DC322	46°24.2	51°53.9	Crozet	4.21	105-95

¹BB = "Okean" grab; CB = Blake trawl; CP = Beam trawl; DC = Charcot dredge; DR = Rock dredge; DS = Sanders epibenthic dredge.

ilar or identical shape, size, content (4 young occupying the major part of the available volume) and biological substrate (skate egg capsule). This means a drastically reduced number of lecithotrophic larvae, and a remarkable association between the egg laying of *P. pulcher* and the egg laying of skates.

In the sample 95/DC233, a single similar capsule containing 2 young was attached at the inner surface of a large shell of *Malletia gigantea* (Figure 4).

The large size of the young contained in these capsules (7.4 mm in length, and 5.1 mm maximum diameter) and the presence of an empty capsule indicate imminent hatching: the first collection was made on April 15, and the second and third on March 7 and 11. Thus, hatching obviously occurs at the end of the austral summer or at the beginning of the austral autumn.

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The Role of Passive Dispersal in the Distribution of Hemipelagic Invertebrates, With Examples from the Tropical Pacific Ocean

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(3 Text figures)

INTRODUCTION

THE FOSSIL RECORD contains numerous examples of anomalous biogeographic distributions. In the past, the classic approach in explaining these anomalies has been to invoke largely nonbiological mechanisms, such as physical land or sea barriers. More recently, VALENTINE (1973) and others have attempted to relate the distribution of marine faunas to seafloor spreading and to the changing position of the continents through the Phanerozoic. However, the causes of many of these biogeographic anomalies can be more adequately explained by determining the effects of biological mechanisms on dispersal. Unfortunately, the use of the biological approach in solving faunal anomalies in the fossil record has been generally ignored by the paleontologist.

The distribution of Recent molluscan faunas in the northcentral Pacific around Hawaii and along the west coast of Central America is characterized by a number of anomalous associations. It is our contention that these faunal anomalies largely reflect the distributional patterns resulting from dispersal by currents rather than the biogeographic end products necessitated by the long-term effects of plate tectonics. Because many of these anomalies can be explained by the existing oceanic circulation phenomena, it is the focus of this review to examine the role of larval dispersal across broad expanses of deep water as a biological vehicle that contributes to the occurrences of

faunal anomalies. The recognition of these biogeographic relationships provides the framework for a potential model to explain similar faunal associations in the fossil record.

DISPERSAL OF HEMIPELAGIC INVERTEBRATES

The distributional patterns of major components of the marine biota are reflections of oceanic circulation operating temporally as a dispersal mechanism. An understanding of how different organisms are dispersed by currents is essential to the understanding of marine biogeography. Dispersal of marine life may be divided into 2 broad categories (passive and active). Passive dispersal may be defined as: dispersal of planktic organisms by ocean currents during the larval stage of development or by rafting on floating debris. Planktic organisms, in turn, may be divided into 2 groups: those organisms which are totally pelagic spending their entire lives in the plankton and the larvae of benthic species which spend only a portion of their life cycle in the plankton. This is in contrast to the mode of active dispersal of nekctic animals which have the capability to control their movements. In most cases, these nekctic species remain within a particular water mass or current. The major difference between nekctic and planktic organisms in terms of dispersal is that nekctic species have the poten-

tial to control largely their movements and can swim against the flow or leave a given current.

The direction of dispersal is unidirectional and linear, owing to the inability of larvae to swim actively and to move against the flow of the current. Thus, currents may be viewed as distinct one-way corridors of dispersal and at the same time as barriers to dispersal (ZINSMEISTER, 1974b). The importance of distance as a barrier to dispersal in the sea is well known (EKMAN, 1953). The greater the distance, the less likely an organism is able to survive transport. In the case of invertebrates with hemipelagic larvae, this is only partly true. Of greater importance is the direction of circulation. No matter how close two points are, if the current is not flowing in the proper direction, the organism will not be able to bridge the gap. The significance of dis-

tance as a barrier depends on the length of the pelagic stage and the velocity of the current.

Until relatively recently, it was commonly believed that transport of larvae over long distances was rare (EKMAN, 1953, and THORSON, 1961). Recent papers (SCHELTEMA, 1966, 1968, 1971, 1972, 1974, 1977, and ROBERTSON, 1964) have shown that many groups of invertebrates have pelagic larvae that can remain in the plankton for as long as a year. SCHELTEMA (1971), in a discussion of trans-Atlantic dispersal of benthic mollusks, proposed the term teleplanic for larvae that are capable of remaining in the plankton for extended periods of time. For teleplanic larvae distance plays a secondary role to the direction of circulation as a barrier to dispersal.

The velocity and direction of oceanic currents may vary

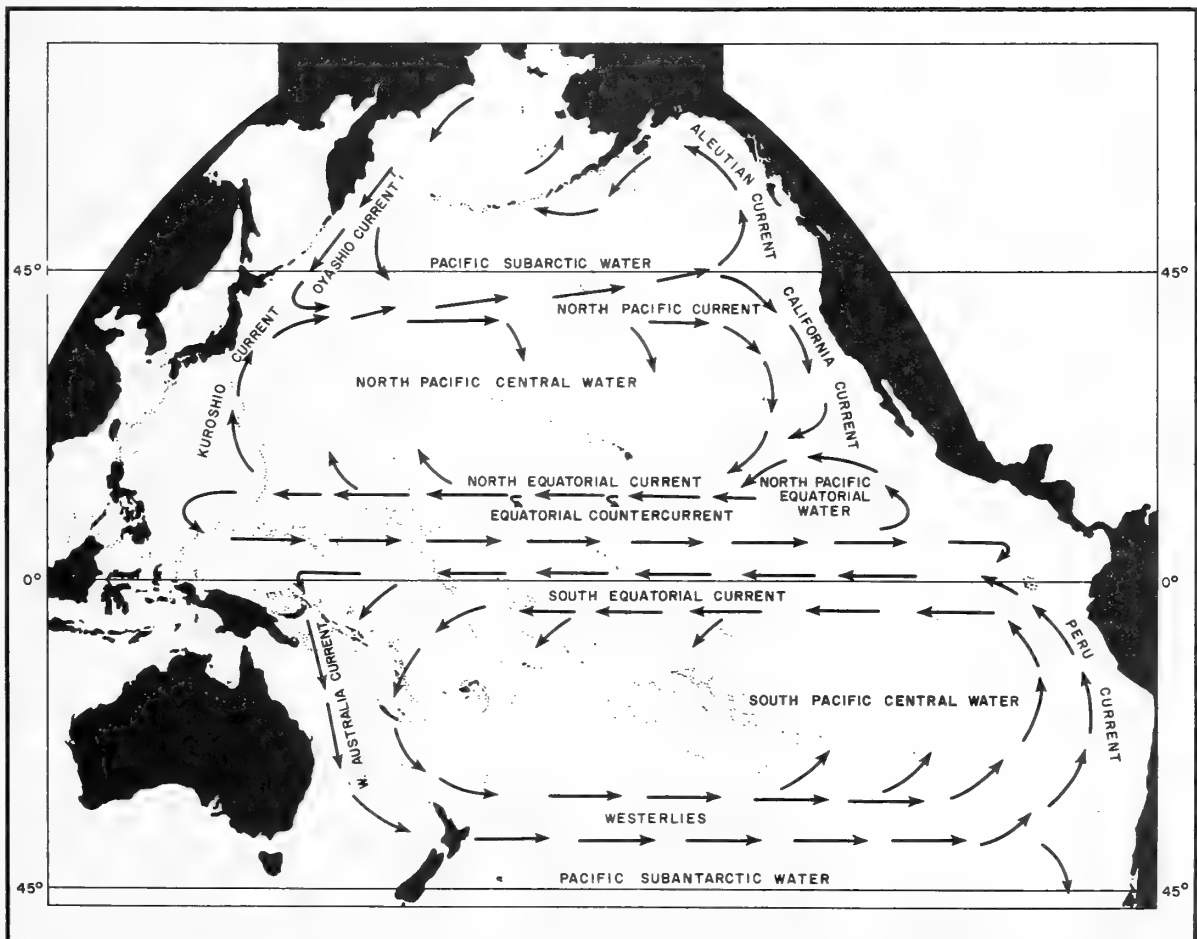


Figure 1

Pacific Ocean Currents (AMERSON & SHELTON, 1976)

considerably over a period of time. The causes of these variations in circulation are not well understood, but are likely to be in response to major short-term climatic fluctuations. These brief periods of atypical circulation play an important role in the distribution of marine life. Such episodes of abnormal transport are here referred to as dispersal pulses and may allow the establishment of a population hundreds of kilometers beyond the taxon's normal range. ZINSMEISTER (1974a) cited several examples of anomalous occurrences of modern Panamic mollusks in southern California well north of their expected normal range. Each of these occurrences could be related to an earlier period of abnormal oceanic circulation off the coast of southern California.

Consideration of the source of pelagic larvae is also important in the discussion of dispersal corridors. Basically, the source of larvae may be divided into 2 categories: primary and secondary loci of dispersal. The primary locus of dispersal is the region that supplies the major proportion of larvae to the dispersal corridor. A secondary locus of dispersal is defined as an area within the path of the corridor that receives larvae from a primary source. These regions, where breeding populations have become established, act as new loci of dispersal within the corridor. The net effect of these secondary loci of dispersal within the corridor is to lengthen the corridor and to facilitate the extension of the range of those organisms with short larval stages, which would not be able to cross large distances of open ocean.

The following examples will serve to illustrate the application of the principles of passive dispersal to explain apparently anomalous distribution of some Recent mollusks in the Pacific Ocean (Figure 1).

WESTERN CENTRAL AMERICA

The modern molluscan faunas of the equatorial Pacific may be divided into 2 large zoogeographic regions. The Indo-Pacific region encompasses the central and western Pacific. It is separated from the Panamic region of the eastern Pacific by 5000 km of open ocean. This expanse of open sea is referred to by EKMAN (1953) as the East Pacific Barrier and has existed at least since late Pliocene time when the eastern-most central Pacific islands essentially had attained their position in the basin (DANA, 1975; VERMEIJ, 1978). The Panamic molluscan province extends from near the head of the Gulf of California southward to Ecuador. KEEN (1971) listed a fauna of approximately 3300 species of mollusks from the Panamic Province. Within this large faunal assemblage a small Indo-Pacific element (less

than 1%) has been recorded (BERTSCH, 1973; EMERSON, 1978; VERMEIJ, 1978). Significantly, these Indo-Pacific species, except for rare occurrences on the continental shelf from Mexico to Ecuador, are restricted to the offshore islands. Furthermore, the presence of an Indo-Pacific element in the Panamic Province is in sharp contrast to the absence of Panamic species in the Indo-Pacific Province (EMERSON, 1967).

This seemingly anomalous occurrence of Indo-Pacific species on the islands off the west coast of Mexico and Central America raises several interesting questions concerning the biogeographic distribution of marine life in the equatorial eastern Pacific.

- (1) How did these shallow-water mollusks manage to cross 5000 km of open ocean of the East Pacific Barrier?
- (2) What has prevented Panamic species from crossing the East Pacific Barrier to the Central Pacific?
- (3) Why, for the most part, are all the Indo-Pacific taxa restricted to the offshore islands?

Analysis of the 52 species comprising the Indo-Pacific element reveals that these are shallow-water inhabitants consisting of 45 gastropod and 7 bivalve species (BERTSCH, 1973; EMERSON, 1978). All but one of the bivalve species are either attaching or boring epifaunal species. In answering the first question of how did the Indo-Pacific shallow-water taxa manage to cross the East Pacific Barrier, 3 primary mechanisms are considered: (1) migration along the seafloor, (2) "island hopping" from seamount to seamount, and (3) drifting across as larvae or on floating debris.

The vast expanse of abyssal water and the absence of guyots between the easternmost Polynesian Islands and the continental shelf of the West American shores presumably effectively eliminates seafloor migration and "island hopping." Thus, the prevailing eastward flowing currents are the most plausible mechanism for the transport of these shallow-water species across the eastern Pacific barrier in the form of drifting larvae, or by attachment of eggs, larval or adult forms to floating debris. Other vehicles of dispersal, such as attachment to birds and nektic organisms, as well as transport by man, may serve as secondary agents of dispersal (HERTLEIN & EMERSON, 1953).

An examination of the oceanic circulation in the eastern central Pacific (Figure 2) serves to support this assessment. Oceanic circulation in the central eastern Pacific may be resolved into 3 broad components: (1) a fairly strong eastward flowing system of currents carrying warm tropical water along and slightly north of the equator, (2) two less well-defined but broader westward flowing cool water currents on either side of warm east-flowing currents, and

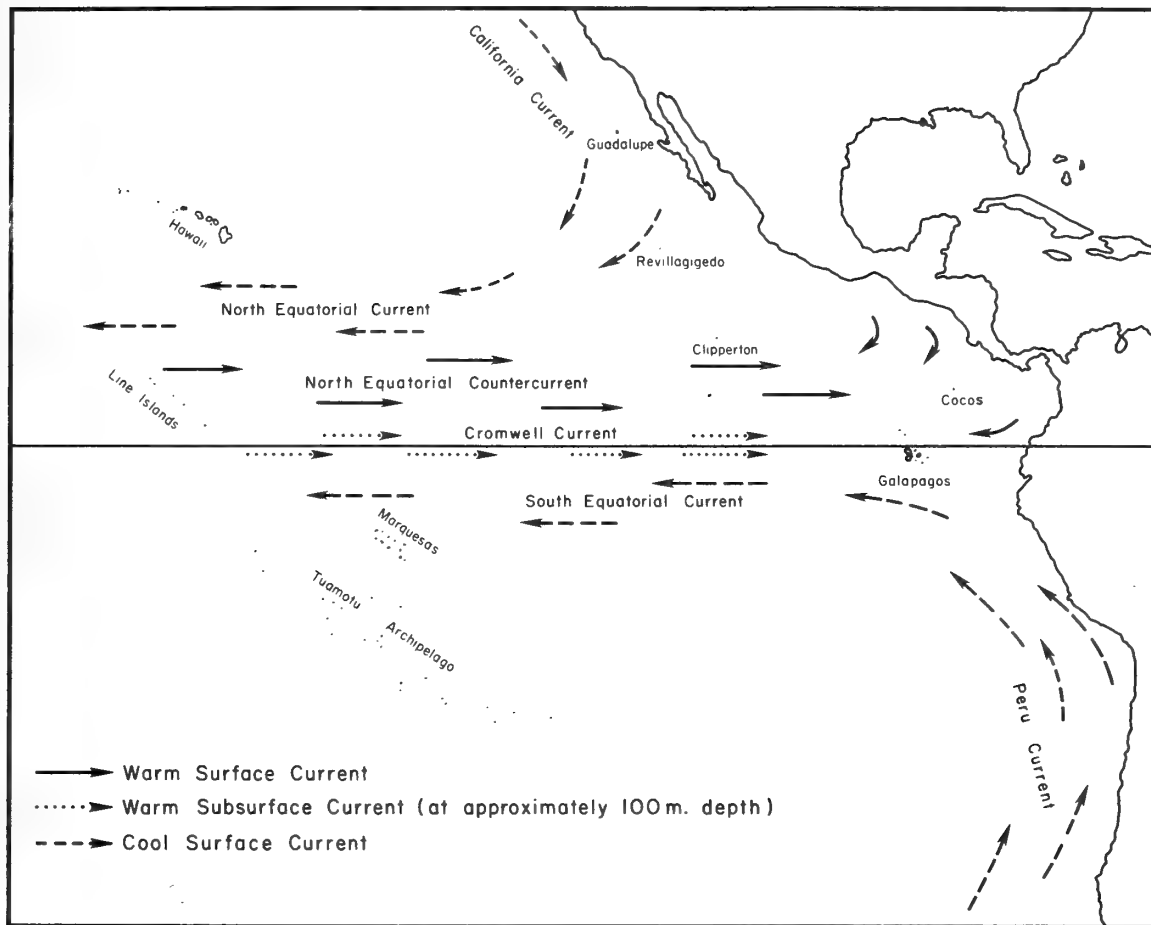


Figure 2

Major Ocean Currents in the Eastern Central Pacific
(modified from AMERSON & SHELTON, 1976)

(3) a smaller region of westward flowing currents originating near the coast of Central America and disappearing about 800 km off the coast.

The warm east-flowing water consists of 2 well-defined currents: North Equatorial Countercurrent and the Cromwell Current. The North Equatorial Countercurrent originates in the western and central Pacific and flows eastward approximately 5° to 7° N of the equator. The strength of the North Equatorial Countercurrent varies considerably during the year. Particularly during the summer months (actually July through November) it is especially well-developed and may have velocities up to 2 km per hour. This warm surface current brings plankton-laden water from

the central Pacific to approximately 1100 km or 1300 km off the coast of Central America. In this region, it becomes ill-defined and disappears.

The Cromwell Current is a narrow, well-defined tongue of easterly flowing water along the equator at a depth of approximately 100 m. This rapidly moving current may attain velocities of 5 km an hour (TAFT, *et al.*, 1974). SCHELTEMA (1968) discussed an analogous current in the Atlantic and noted large numbers of larvae were transported by it eastward across the Atlantic and he also pointed out its possible significance to biogeography. There are not data available about plankton distribution by the Cromwell Current in the Pacific, but presumably it

is an important conveyor of plankton eastward from the western and central Pacific.

The major westward flowing currents consist of 2 broad cool water currents: the Peru Oceanic Current and the California Current. The Peru Oceanic Current is the north extension of the Humboldt Current. This major current carries cool subantarctic waters along the coast of South America and turns westward at about 10° S latitude and then becomes the South Equatorial Current. The cool temperature California Current flows southward along the coast of western North America and then swings almost due west at about 10° N latitude and becomes the North Equatorial Current. The other westward flowing current consists of a weak and ill-defined system of currents developing along the coast of Guatemala and Panama. This current system appears to consist of a large clockwise eddy in the Gulf of Panama with the prevailing flow to the southwest (CROMWELL & BENNETT, 1959). This southwest flow gradually disappears about 800 to 1000 km west of the coast of Central America.

The prevailing current patterns thus offer a ready explanation for the anomalous occurrence of Indo-Pacific mollusks in the eastern Pacific and for the absence of any eastern Pacific species in the central Pacific. The only warm currents in the central eastern Pacific are the east-flowing North Equatorial Countercurrent and the Cromwell Current along the Equator. These 2 currents are excellent examples of dispersal corridors which bring warm plankton-laden water to the eastern Pacific. The limited number of Indo-Pacific elements in the East Pacific faunas reflects the great distance across the central-eastern Pacific Ocean. Only those benthic species with extremely long pelagic larval stages are able to cross this vast expanse of open water. The absence of more Indo-Pacific species on these offshore islands is probably related to the lack of suitable habitats with available ecological niches and specific food sources, and to competitive pressures (*cf.* DEICHMANN, 1959; EMERSON, 1967; BACKUS, 1968; DANA, 1975; VERMEIJ, 1978).

The absence of warm westward flowing currents has prevented Panamic species with long pelagic stages from reaching the Central Pacific. The only westward flowing currents across the East-Central Pacific are the cool temperate California and Peru Oceanic currents. Any cool water species with a long distance larval stage would be unable to find suitable cool temperate habitats if it reaches the nearest land or shallow-water areas (Marquesas or Line Islands) in the central Pacific. Therefore, the absence of eastern Pacific faunal elements in the central Pacific seems to reflect: (1) no warm westward flowing current for tropical Panamic species and (2) an absence of suitable habitats, including the lack of non-coral, hard substrates

(BAKUS, 1968), for any cool water species that might be transported across the expansive eastern Pacific (Ekman's Barrier), rather than the contention of BRIGGS (1974) that the west American forms are not as interfaunistically competitive as the Indo-Pacific forms.

The answer to the final question concerning the meager representation of Indo-Pacific mollusks on the west coast of the American mainland may be found in the presence of largely westward flowing currents off Central America (Figure 3). Despite the narrow gap (500 to 1000 km) from the offshore islands to the coast of the mainland only 16 of the 52 Indo-Pacific species reported to occur in Eastern Pacific waters are known from the West American coast (EMERSON, 1978; BERTSCH, 1973). Therefore, it seems probable that the westward flowing shore currents are acting as a partial barrier to dispersal eastward to the mainland for the populations that occur on the offshore islands. Furthermore, should the larvae of Indo-Pacific coral-reef associated organisms reach the mainland, the impoverishment there of this biotope would be a further limiting factor for the establishment of coral-loving species (EMERSON, 1967).

HAWAIIAN ISLANDS

The Hawaiian archipelago consists of a chain of volcanic islands, atolls, and shoals extending 2600 km from the southeast to the northwest. It is one of the most isolated island groups in the Pacific region. It is situated in the mid-Pacific some 5400 km from Japan, 3200 km from California and 700 km from the nearest island.

The Hawaiian molluscan fauna is characterized by a number of anomalous features. The composition of the Indo-Pacific faunal province within the Pacific Basin may be divided into 2 major elements, the Western Pacific and Central Pacific elements. Normally, the farther east an island group is located, the smaller is the percentage of Western Indo-Pacific species (KAY, 1967). The Hawaiian islands, although the most eastward located island group, have an anomalously high percentage of Western Pacific species. KAY (1967) further points out that the Hawaiian fauna is relatively small, consisting of only about 900 species. Faunas from insular groups in the western Pacific at approximately the same longitude normally have 2 to 3 times as many species. The ratio of gastropods to bivalves in the Hawaiian Islands conforms to Kay's observation that the farther east an island group is, the higher the ratio of gastropods to bivalves becomes. Lastly, the percentage of endemic species in the Hawaiian fauna is significantly large, approaching 20%, for insular faunas in the Indo-Pacific.

Following the classical approach to insular biogeography, the origin of the Hawaiian fauna would be interpreted to be from the southwest. Immigrants would have reached Hawaii by using the many islands or seamounts in the southwest and central Pacific as stepping stones in their eastward radiation. This is the most likely case for much of the terrestrial biota, though aerial immigration by the agency of birds, insects and cyclonic winds is suggested for the smaller land snails (SOLEM, 1974; VAGVOLGYI, 1976), but these vehicles were largely rejected by CROIZAT (1978). CLARK (1949) expressed the opinion that the Hawaiian ophiuroid fauna was derived from the central Pacific by insular hopping via the Caroline and Marshall Islands. KAY (1967), based on MENARD's (1964) studies of the geological history of the Pacific, adopted Clark's hypothesis of a center of origin from the southwest and suggested that the Marcus-Necker ridge may have acted as stepping stones for introduction from the west. The present water depth of the crest of the Marcus-Necker ridge is an average depth of 1463 to 1828 m. It is difficult to conceive that shallow-water species could have used the Marcus-Necker ridge as stepping stones to Hawaii because of the great water depth. It will be shown later that the existing current pattern does

not support the thesis for larval drifting from the southwest to Hawaii.

Insular marine communities are less dependent than terrestrial communities on chance dispersal. The composition of insular marine communities depends largely on the location and distance from the nearest source of pelagic larvae. Since oceanic currents constantly transport larvae, the composition of an island marine fauna can be predicted. The closer the island is to the source area, the more likely the faunas of the 2 areas will be the same. The farther the island is from source area the more depauperate the fauna is and its composition is dominated by species with teleplanic larvae.

Examination of oceanic circulation patterns (Figure 3) suggests that the Hawaiian marine fauna was largely derived from the west across the 5400 km of open ocean. The warm Kuroshio Current is the major current in the western North Pacific, where it flows northeast from Formosa along Japan and splits into 2 branches at approximately 35° N latitude. The northern branch continues flowing northward, gradually turning southward in the north Pacific, and it becomes the California Current. The southern branch (Kuroshio Southern Extension) flows almost due

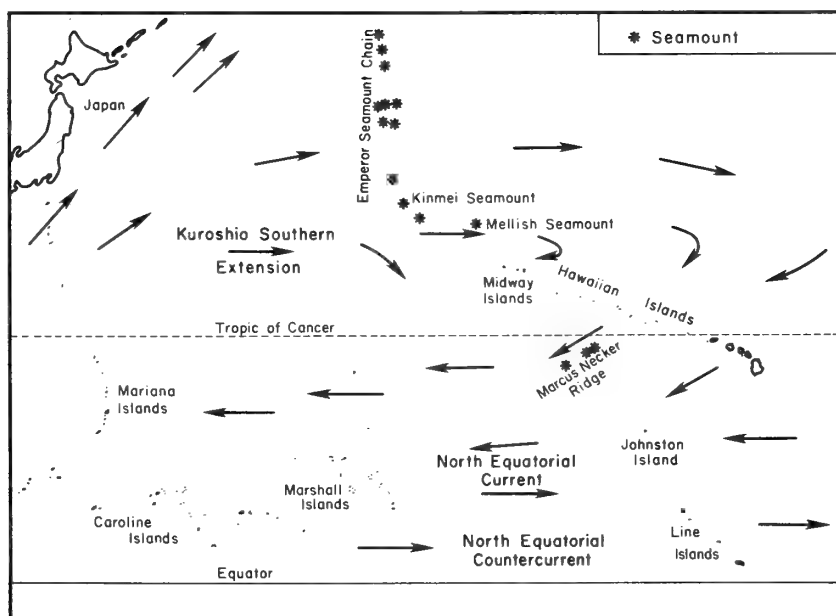


Figure 3

Major Ocean Currents in the Western Central Pacific
(modified from AMERSON & SHELTON, 1976)

east. In the vicinity of longitude 155° to 160° E, a considerable amount of water is deflected southward forming the Kuroshio Countercurrent (SVERDRUP, *et al.*, 1942). By this vehicle a large amount of warm tropical plankton-laden water from the western Pacific is brought to the region around Hawaii.

Johnston Island, located 720 km to the southwest of Hawaii, lies in the westward flowing North Equatorial Current. The northernmost Line Islands lie in the east flowing Equatorial Countercurrent and had attained this position before the end of the Pliocene (DANA, 1975). Any larvae originating from these islands are transported by the prevailing currents away from Hawaii. It therefore seems highly unlikely from oceanographic evidence that the modern Hawaiian molluscan faunas originated from the southwest.

It is interesting to note that the molluscan fauna of Johnston Island is very closely related to Hawaiian faunas (REHDER, in AMERSON & SHELTON, 1976). Because of its location down current from Hawaii (Figure 2), it seems likely that instead of acting as a filter bridge for migration to Hawaii (AMERSON & SHELTON, 1976), its fauna was largely derived from the Midway-Hawaiian chain.

A western Indo-Pacific source area for the modern Hawaiian molluscan faunas by means of pelagic larvae is supported by biological evidence as recorded by the composition of the fauna. KAY (1967), in a review of the Hawaiian molluscan faunas, noted that these insular faunas are very attenuated. The total number of molluscan species from Hawaii is slightly more than 900 species as compared to "... New South Wales and western America, which are about the same latitude above and below the Equator as the Hawaiian chain, have molluscan faunas of approximately 2000 species, in the Philippines about 3000 species ... Okinawa which is close to the continental area, has a molluscan fauna of about 1700 species." The most probable cause for this observed attenuation may be the fact that only those species with long distance larvae are able to cross the western Pacific. Kay further noted that the Hawaiian fauna is characterized by a very high gastropod to bivalve ratio (Table 1). There are two possible explanations for this anomalous ratio. The low number of bivalves may reflect the absence of suitable habitats in insular situations, especially the lack of well-developed, sandy substrates (THORSON, 1950; TAKI, 1953). THORSON (1961) stated that the bivalves were "... among all the groups studied ... [the] one most unfit for long-distance transportation." Therefore, if the source of the fauna is from the west, it would be expected that the number of bivalves reaching Hawaii would be low. In addition, the diversity of the intertidal Hawaiian fauna is quite low. This low

Table 1

Composition of modern marine molluscan fauna of Hawaii (modified from Kay, 1967).

Class	No. of Species	Percentage of Hawaiian Marine Mollusca
Cephalopoda	15	2
Amphineura	5	1
Scaphopoda	9	1
Bivalvia	150	16
Gastropoda		
Archaeogastropoda	38	4
Mesogastropoda	262	29
Neogastropoda	254	29
Opisthobranchia	165	18
		80
Total	719	100%

diversity is clearly illustrated by comparing the diversity of the amphineuran fauna of Hawaii (5 species) with that of other warm water regions in the Pacific. The Aupourian Province of the North Island of New Zealand contains 32 species (POWELL, 1958) while the Panamic Province of the eastern Pacific has 51 species (KEEN, 1971). From the limited number of molluscan developmental studies available, it appears that intertidal species in general tend to have either direct development or very short veliger stages (THORSON, 1961; RADWIN & CHAMBERLIN, 1973).

The composition of its molluscan fauna seems to support strongly an origin of the Hawaiian marine faunas from the western Pacific by means of pelagic larval transport by the Kuroshio Southern Extension Current. The fauna is dominated by those groups of mollusks which are characterized by having long distance larvae. Those molluscan groups with either direct development or short pelagic larval stages such as the archaeogastropods are conspicuous by their low diversity (Table 1).

Endemic species constitute a prominent element (20%) of the Hawaiian molluscan fauna. KAY (1967) noted that endemism was highest among western Indo-Pacific and intertidal species. BRIGGS (1966) proposed that insular endemism of marine faunas could be related to changes of sea temperatures during the last glacial period. "Those islands that demonstrate the least amount of endemism were probably exposed to the greatest decline in surface temperatures." In those insular regions where significant temperature changes occurred, the fauna were displaced and they have only recently been repopulated. The length

of time since the repopulation presumably has not been sufficient for evolutionary changes to have occurred. Conversely, in insular areas where temperatures have remained constant for long periods, there would supposedly be sufficient time for new taxa to evolve and these areas would be characterized by high endemism. This may have been the cause of the endemism in Hawaii, but this diversity may also be explained by changes in sea level (ZINSMEISTER, 1973).

Eustatic fluctuation in sea level during the Pleistocene approached 200 m. These changes resulted in the shallow water seamounts north of Hawaii becoming islands or shoals. The present depth of the Mellish Seamount at the extreme north end of the Hawaiian archipelago is 117 m and the Kinmei Seamount (southern end of Emperor Seamount chain) has several peaks with water depths of less than 183 m. The presence of islands and shoals in the Pleistocene would have reduced the distance of open sea between the present islands in the western Pacific and the modern Hawaiian Islands. This would have enabled species with relatively short pelagic larval stages to use these islands as filter bridges in their eastward journey. Removal of these stepping stones with the rise of sea level would have effected molluscan dispersal across the western Pacific by widening distances between insular land in either of 2 ways: (1) caused the development of a barrier (distance) to all drifting larvae, or (2) caused the development of a barrier to those species with relatively short pelagic larva stages. In the first case, endemism could be explained by differential rates of evolution. In the second case, only those species with short larval stages would be prevented from reaching the Hawaiian Islands. The result would be that those species with shorter pelagic stages would be effectively isolated from the western Pacific and would follow their own evolutionary course in the Hawaiian Islands. Species with long distance larvae would not be affected by the removal of these islands and would retain their genetic identity with the western Pacific faunas. KAY (1967) noted that the highest endemism occurs in the intertidal species. This would be the group that would show the effect of the formation of the barrier at the end of the Pleistocene because intertidal species generally have the shortest pelagic larval period. The development of this partial filter to eastward dispersal from the western Pacific appears to be the primary cause for the endemism in the Hawaiian molluscan fauna. Although the level of endemism is relatively high (20%), these elements are largely limited to taxa on the specific and sub-specific level, which suggest a relatively recent formation of the barrier.

CONCLUSION

The dynamics of passive dispersal by currents of the larval forms of marine organisms are related to the inability of these larvae to control actively their movements. Larvae may be dispersed by currents only parallel to and with the direction of the flow. Currents may be viewed as one-way corridors of dispersal. The direction of circulation, not spatial distance, is the most critical factor in determining the distribution by currents of these species in the sea. The length of the larval stage and the distance between suitable habitats also serve to limit larval dispersal and to act as a distributional survival factor for species. The biogeographic distribution of benthic invertebrates with pelagic larvae thus may be viewed as a reflection of oceanic circulation patterns operating temporally as a dispersal mechanism. The role of passive dispersal of hemipelagic invertebrates is illustrated by modern and past faunistic distributional patterns occurring in the tropical Pacific Ocean.

The role of passive dispersal as a vehicle for the introduction of faunal elements into existing and past assemblages of organisms must also be interpreted in the light of geologic events within a framework of chronology. Without temporal considerations, the student of biogeography may draw erroneous conclusions owing to the multiplicity of factors that influence distribution. A realization of the significance of the function of currents on the distribution of life in the sea, however, provides an additional tool for the paleontologist to interpret biogeographic history. Based on the present knowledge of the oceanic basins and the position of the continents for the most of the Phanerozoic, it is possible to approximate the general circulations within the basins. Utilization of the principles of passive dispersal should permit a better understanding of paleobiology.

ACKNOWLEDGMENTS

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Three New Opisthobranch Records for the Hawaiian Islands

BY

HANS BERTSCH¹ AND SCOTT JOHNSON²

(1 Plate)

THROUGH EXTENSIVE COLLECTING by subtidal SCUBA diving on the island of Oahu, we have discovered several species of opisthobranch mollusks previously unreported from the Hawaiian Islands. This note documents the presence of a cephalaspidean and 2 nudibranchs in several diverse, subtidal habitats on the northern and southern coasts of Oahu.

CEPHALASPIDEA

GASTROPTERIDAE

Gastropteron flavum Tokioka & Baba, 1964

Material: 2 specimens, 12 m deep, Pupukea, Oahu; *leg.* Judith Bertsch and Larry Targett, 4 June 1978.

Description: The 2 living animals were 4.5 and 4.75 mm long (1.5 mm wide). The yellow and black coloration was quite distinctive (Figure 1). Their overall body color was a brilliant yellow. The cephalic shield rises to a prominent, posteriorly directed funnel. The posterior third of the shield is covered with a rich black marking that surrounds the base of the funnel. The distal tip of the funnel is yellow. One animal had a black swath of color leading anteriorly, ending in an irregular black patch on the cephalic shield in front of the eyes. The postero-dorsal region is colored black. These markings give the overall appearance of a careless painting technique, where the painter did not smooth and conceal his brush strokes. A knob-like, yellow protuberance extends from the midst of this posterior black area.

Discussion: The type locality of *Gastropteron flavum* is Sagami Bay, Japan; it also has been reported from the Japan Sea side of Honsyu Island (TOKIOKA & BABA, 1964:

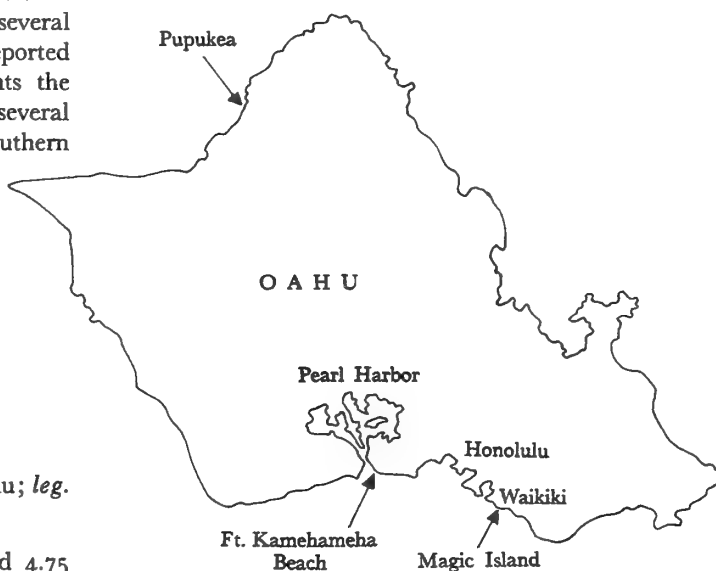


Figure 3

Map of Oahu, showing the 3 collecting sites mentioned in the text
Drawn by A. D'Attilio

215; BABA & TOKIOKA, 1965: 40). CARLSON & HOFF (1974: 346-347) report collecting *G. flavum* along the island chains south of Japan: Maug, Uracas, Asuncion, Agrihan and Pagan, Mariana Islands; Bile Bay, Merizo, Guam; Moen, Truk, Eastern Caroline Islands; and Koror, Palau, Western Caroline Islands. The 2 specimens collected on the northern shore of Oahu (Figure 3) represent an eastward range extension of over 3500 miles [over 5800 km] from the nearest previously reported collecting locality.

Pupukea is a small bay north of Waimea, with relatively calm water during the summer months. In winter, high surf conditions make diving extremely dangerous. The inlet is sandy bottomed, with numerous ledges and mounds of coralline limestone. The rocky substrate is usually fairly

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clean of sediment and underwater visibility can exceed 15 m. The bench reef around the margin of the inlet has numerous subtidal ledges, caves and overhangs along its vertical face that are covered with a wide diversity of algae, sponges, and coelenterates. In the narrow intertidal region occur patches of the alcyonarian *Anthelia edmondsoni* (Verrill, 1928) and subtidally the orange ahermatypic coral *Tubastrea coccinea* Lesson, 1831, can be found under the deeper ledges. Numerous mobile benthic organisms occur also at Pupukea, including the prosobranchs *Latirus nodatus* (Gmelin, 1791) and *Cypraea maculifera* (Schilder, 1932), and the nudibranchs *Phyllidia varicosa* Lamarck, 1801, and *Chromolaichma youngbleuthi* (Kay & Young, 1969). The main impression that a SCUBA diver has of the area is of fairly clean, exposed surfaces, with the semi-protected crevices, ledges and caves heavily covered with sessile and crawling benthic forms.

NUDIBRANCHIA

CHROMODORIDAE

Hypselodoris infucata (Rüppell & Leuckart, 1828)

Material: 1) 1 specimen, shallow subtidal, Fort Kamehameha Beach, Oahu; *leg.* Michael de Gruy, 17 August 1977

2) 1 specimen, Ft. Kam.; *leg.* Scott Johnson, 24 September 1977

3) 8 specimens, Ft. Kam.; *leg.* Scott Johnson, 15 October 1977

4) 1 specimen, Ft. Kam.; *leg.* Judith Bertsch, Hans Bertsch, 13 May 1978

5) 1 specimen, Ft. Kam.; *leg.* Hans Bertsch, 6 June '78

6) 3 specimens, Ft. Kam.; *leg.* Judith Bertsch, Hans Bertsch and Larry Targett, 11 June 1978

All the specimens were collected in the shallow subtidal region of Fort Kamehameha Beach (Figure 3), in approximately 1 - 10 m of water.

Description: This species has been the subject of lengthy discussions in several recent papers on the Indo-Pacific chromodorid nudibranchs. The animals from Hawaii (Figure 2) have a cream background color. The notum is

covered with numerous navy blue-black dots. A suffuse blackish-gray (blue-gray) color envelops the notum to a varying degree on each animal; this indistinct color is usually concentrated around the black dots and gives a dark appearance to the animal. The back is liberally sprinkled with small orange-yellow dots, and an indistinct patchwork of white occurs longitudinally down the center of the notum. The rhinophores are red, with a white base below the perfoliations. The gills are red, and have white on the distal portions of the pinnules.

Our material closely matches the animals described by EDMUNDS (1971: 375 - 379) and RUDMAN (1977: 385 - 387). They are, however, very different from those described by THOMPSON (1972: 395 - 398), which are probably representatives of 2 other species, as RUDMAN (*op. cit.*: 387 - 388) recently suggested.

Discussion: *Hypselodoris infucata* has been reported from the Red Sea (type locality), East Africa (Zanzibar, Dar es Salaam) and South Africa (cf. EDMUNDS, 1971, for these references); southern Australia (BURN, 1962: 151 - 152); the Philippine Islands (BERGH, 1877: 482 - 484); New Caledonia and Fiji (RUDMAN, 1977: 387). The specimens collected in Hawaii are a range extension of over 5 000 km; *H. infucata* has now been reported from the farthest eastern and western perimeters of the Indo-Pacific marine faunal province. Its occurrence in southern Australia is surprising zoogeographically, since that area is outside the tropical Indo-Pacific faunal province (see VALENTINE, 1973: 356). However, the occurrence of this species in subtropical Hawaiian waters gives further evidence of its range of physiological and thermal tolerances.

So far in Hawaii, *Hypselodoris infucata* is known only from the shallow subtidal region at Fort Kamehameha Beach, on the northeastern edge of the entrance to Pearl Harbor. The area can be divided into 4 distinct marine habitats: 1) Closest to shore there is a broad, shallow mud-flat area (over which the Hawaiian stilt, *Himantopus himantopus knudseni*, feeds at low tide), with infrequent rocky areas covered by the algae *Padina* and other genera. 2) Farther seaward is a limestone reef area, exposed at low tides, which consists of a fore-reef pitted with pockets of the urchin *Echinometra mathaei* (de Blainville, 1825) and a coral rubble back-reef area, where the rocks are covered with algae, sponge, and tunicate growths. The gastropods *Cypraea caputserpentis*

Explanation of Figures 1 and 2

Figure 1: *Gastropod flavum* collected at Pupukea; photograph by Scott Johnson

Figure 2: *Hypselodoris infucata* from Fort Kamehameha Beach; photograph by Hans Bertsch



Figure 1



Figure 2

Linnaeus, 1758, and *Dolabrifera dolabrifera* (Rang, 1828) occur abundantly in this area. On boulders at the seaward edge of the reef are numerous cryptically-camouflaged specimens of a new species of chiton (*Plaxiphora* sp.) and, more rarely, *Ischnochiton petaloides* (Gould, 1846). 3) In front of the limestone fore-reef is an immediate 2 m drop-off to a shallow subtidal coral rubble area intermingled with a sandy-silt bottom. This area extends towards the main channel, slowly sloping downwards. Characteristic gastropods are *Cypraea teres* Gmelin, 1791, and *C. helvola* Linnaeus, 1758, on the sponge-covered undersides of the rocks and rubble. Common sponges include *Zygomyscale parishi* (Bowerbank, 1875) and the boring *Clione vastifica* Hancock, 1849. 4) At about 6 m deep, the coral rubble abruptly ends at a cliff face dropping vertically 6 or more meters to a steeply sloping fine silt substrate (a diver can sink 10 cm or more into this extremely fine mud-silt) that continues to the bottom of the dredged entrance to Pearl Harbor. Numerous sponges cover the cliff face, and more deeply, there are periodic outgrowths of sponge among and under the sloping silt bottom. *Hypselodoris infucata* has been found in the shallow subtidal regions (3 and 4), from depths of 2 - 14 m. This region is markedly different from the clear water and sand or rocky-limestone substrate of Pupukea. However, both areas have little live coral cover, and when carefully searched, yield a diversity of opisthobranch and prosobranch species.

Hypselodoris maridadilus Rudman, 1977

Material: 1 specimen, 2 m deep, Magic Island, Ala Wai Canal, Honolulu, Oahu; *leg.* Hans Bertsch, 6 January 1978.

Description: The living animal was about 26 mm in total length. The animal's coloration was a pale yellow ground color, with rich reddish-violet longitudinal lines and mantle edging; gills and rhinophores were orange.

Discussion: This species has been reported from Africa (Kenya, Tanzania and South Africa) (RUDMAN, 1977: 359, 361 - 362) and Japan (BABA, 1953: 209 - 211). The specimen from Oahu represents an over 7000 km range extension; *Hypselodoris maridadilus* is now known to occur on the extreme east-west peripheries and north of the central region of the Indo-Pacific faunal province.

Magic Island is a man-made landfill island, on the western edge of the entrance of Ala Wai Canal to the sea (Figure 3). There is a rock boulder cliff face (some 15 m from shore), extending from 1.8 to over 10 m deep, ending at the silty, dredged channel bottom. There are numerous

sponges and tunicates growing on the vertical wall; the boulders provide a multitude of crevices, ledges and interstices extending between the fill towards the island. There is a paucity of coral, a heavy amount of suspended particles in the water, and a rich diversity of nudibranch species occurring along the vertical edge of the channel. The habitat is similar to the subtidal area of Fort Kamehameha Beach, which has an equivalent abundance of sessile filter feeders living in water heavily suspended with particulate matter.

The anatomy of both these species of *Hypselodoris* will be described in a paper we are preparing on the chromodorids of Hawaii.

ACKNOWLEDGMENTS

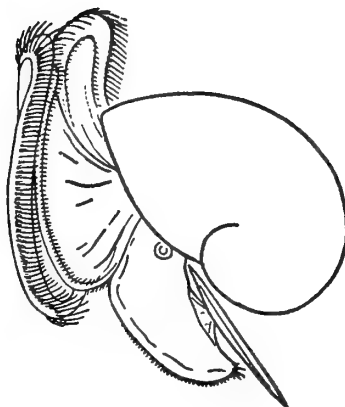
A grant from Earthwatch and the Center for Field Research provided the necessary funds and volunteers that made possible the collection of specimens during June 1978. We are grateful to all the participants on the Hawaiian Mollusks Expedition, especially Larry Targett who collected two of the species in this report. We thank Judith Bertsch for sharing many dives and helping with collecting.

The map was drawn by Mr. Anthony D'Attilio, Department of Marine Invertebrates, San Diego Natural History Museum.

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Onchidoris sparsa (Alder & Hancock, 1846)
in Asturias, Northern Spain¹

BY

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(1 Text figure)

DURING JULY AND AUGUST, 1977, 8 specimens of the little nudibranch *Onchidoris sparsa* (Alder & Hancock, 1846) were collected along the Asturian coast of northern Spain. Although this species was described in 1846, only 5 specimens have been recorded previously (THOMPSON & BROWN, 1976: 102), and they were all collected in the British Isles.

With the finding of these specimens from Spain, we have been able to describe additional morphological characters which augment the original description.

Onchidoris sparsa (Alder & Hancock, 1846)

Material: 1. Verdicio (43° 35'N; 5° 50'W); 2 specimens, under stones in intertidal pools, between a small colony of encrusting bryozoan and a formation of the tunicate *Botryllus schlosseri*.

2. Artedo (43° 30'N; 6° 10'W); 6 specimens, -0.5 m low tide, under stones with encrusting bryozoan (Cribellinidae and Microporidae) on which they feed.

Two of the specimens have been sent to the Paris Museum of Natural History, and the rest are preserved in the Zoology Department of Oviedo University.

Morphological Characters: The largest specimen collected measured 6 mm long. The maximum length known for the species is 8 mm (HUNNAM & BROWN, 1975: 148). The usual color is whitish or somewhat yellowish, with brown or brown-red sparse color patches in between the dorsal tubercles. On the back there is a generally orange-brown central zone which is caused by the visceral pig-

mentation (also visible ventrally in the center of the foot) showing through the skin.

The foot is not furrowed anteriorly. In some animals it slightly protrudes past the posterior mantle edge, especially when the animals move.

Generally the mantle tubercles are widely spaced, short, stout and of wide base, and seldom protrude from the sides of the animal. The tubercles usually have spicules in their bases, and some of them have the apex colored similarly to the mantle patches. In front of the rhinophores and oblique to the long axis of the body, there are 2 bigger tubercles, and in some cases there is a third posterior tubercle.

The rhinophores are completely retractile and in the larger specimens have up to 9 lamellae. The rhinophores are pale yellow and the lamellae are brownish.

The non-retractable gills can have up to 10 unipinnate branchiae distributed around the anus. Usually they are arranged in a horseshoe or quadrangular fashion, in which case 3 anterior tubercles form a line in the transverse axis of the body. In some specimens, the white horseshoe-shaped gills stand out prominently from the brown pigment of the anal region. Usually the anus is located between 2 tubercles, in a richly pigmented region. In some cases an anal papilla is also present.

The mantle spicules are arranged similarly to the pattern found in other species of *Onchidoris*. There is a peripheral band around the margin and an interior region (down the center of the dorsum) in which the spicules lie perpendicular to the long axis of the animal's body. Lengthwise between these 2 regions is a band of oblique (relative to the body's long axis) spicules.

¹ This article forms part of an extensive study of the mollusks of northern Spain, subsidized by the Juan March Foundation

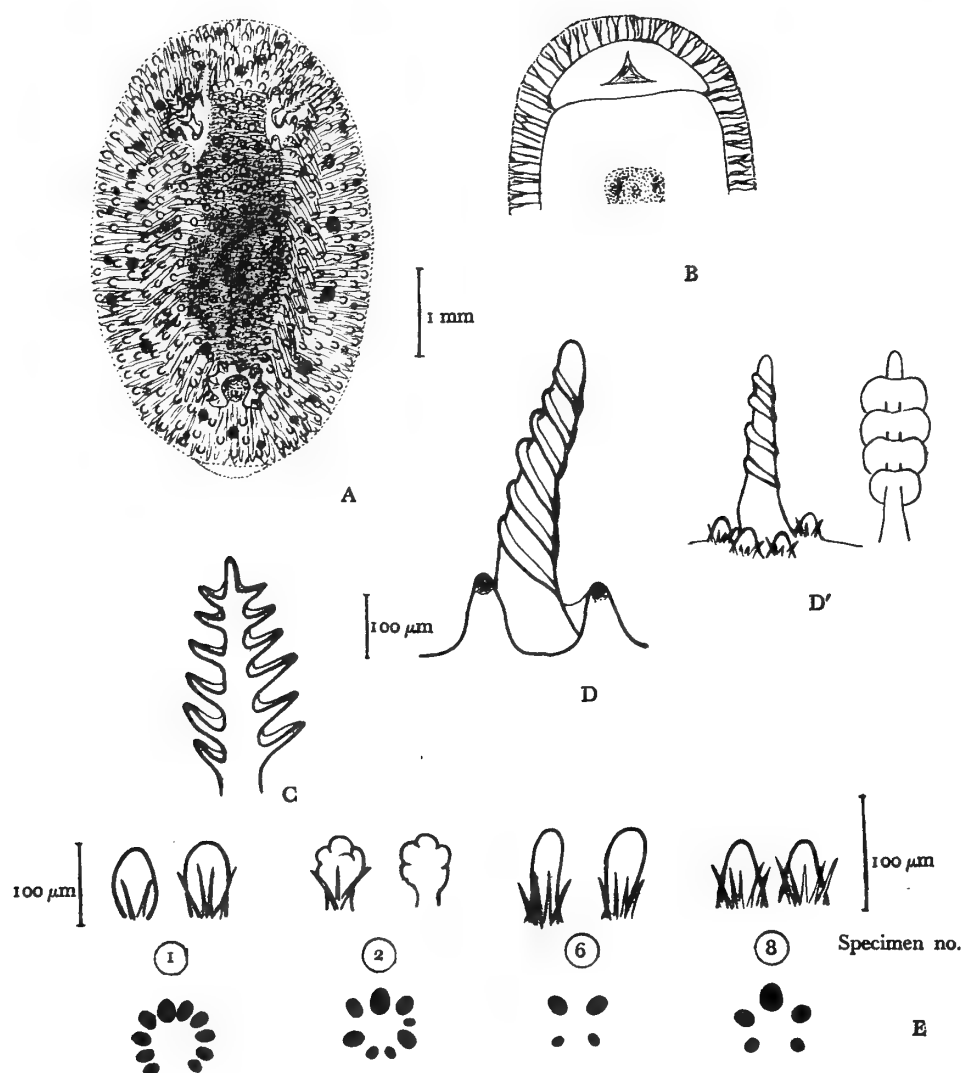


Figure 1

Onchidoris sparsa (Alder & Hancock, 1846)
external anatomy

A Dorsal view of living animal B Antero-ventral portion of
Onchidoris sparsa C Branchial leaf D and D' Rhinophores from the largest and smallest specimens collected E Vari-

ation among the shape of the mantle tubercles and the arrangement of the gills. Circled numbers refer to the specimen numbers in Table 1

Table 1

Morphological variation in specimens of *Onchidoris sparsa*

Specimen Number	1	2	3 and 4	5	6	7	8
Size (length and width in mm)	6 × 3.5	5 × 3	4 × 2.3	3.9 × 2.1	3.2 × 2	2.8 × 1.8	2 × 1
Locality	Verdicio	Artedo	Artedo	Artedo	Artedo	Artedo	Verdicio
Color	yellowish with brown patches	white and yellowish with red patches	white with brown patches	white with brown patches	white with brown patches	white with brown patches	very pale yellow
Foot protruding past posterior mantle edge	yes	no	no	no	yes	no	yes
Unipinnate gills	10	8	7	7	4	6	5
Viscera	brown-pink	reddish	brown-orange	orange	pink	orange	transparent
Rhinophoral lamellae	9	7	6	6	4	6	5
Rhinophoral tubercles	+	reduced	+	+	+	+	very reduced
Pallial tubercles	spherical with a broad base	cauliflower shape and pedunculate	spherical with a broad base	spherical	stout and extended	spherical	conical with rounded apex
Spiculous tubercles	+	some	+	+	+	+	+
Anus between two tubercles	+	+	+	with anal papilla	+	with anal papilla	no

DISCUSSION

The infrequent finding of *Onchidoris sparsa* is probably because of its small size, and its perfect adaptation of shape and color to the substrate of encrusting bryozoans on which it lives.

With this report of *Onchidoris sparsa*, there are now 5 species of the family Onchidorididae known from the Iberian littoral zone:

Acanthodoris pilosa (Müller, 1789)

Onchidoris neapolitana (Delle Chiaje, 1841)

Onchidoris luteocincta (M. Sars, 1870)

Onchidoris sparsa (Alder & Hancock, 1846) and

Onchidoris papillata (Portmann, 1960) (cf. Ros, 1975:

316-318; and 1976: 33-34; ORTEA, 1977a). This is less than half of the 13 species of Onchidorididae known to occur along the European shoreline. There have been few studies of the occurrence of nudibranchs in Spain, so the small number of species may be simply a collection artifact.

The presence of *Onchidoris sparsa* in Asturias lends support to the notion that the distributional range of species currently known only from the English Channel may

actually be much larger. Additional documentation for this idea has been supplied by the recent findings of *Lima-pontia senestra* (Quatrefages, 1844), *Goniodoris nodosa* (Montagu, 1808) and *Doto pinnatifida* (Montagu, 1804) along the Spanish coast (cf. ORTEA, 1977a; 1977b: 86-87, and 1978: 111-113).

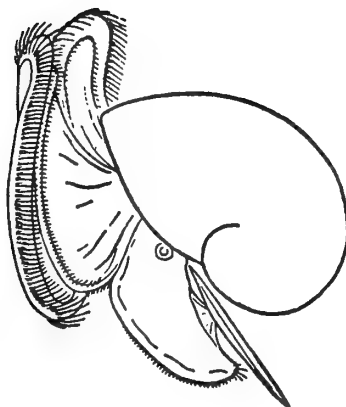
ACKNOWLEDGMENT

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A New Volute from the Western Pacific

BY

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(1 Plate)

DURING A CRUISE of the R. V. "Vauban" on the deep continental shelf of New Caledonia, a new gastropod of the family Volutidae has been dredged. A single, live-taken specimen is present but its characteristics are so different from the other known species of the family that a description is presented herein.

Lyria kuniene Bouchet, spec. nov.

Type Material: Holotype in MNHN²

Type Locality: 22°49'S, 167°12'E (west of Isle of Pines, southern New Caledonia), in 390-395 m; 10 April, 1978

Description: Shell solid, ovate fusiform in outline, composed of 8.5 whorls; the protoconch is bulbous and has 2.5 smooth whorls, thus indicating direct development (Figure 3); the postlarval shell has 6 shouldered whorls with a moderately deep suture. The postlarval sculpture consists of a few distant axial ribs of which there are 9 on the body and penultimate whorls; these ribs are a little more closely spaced on the first 2 postlarval whorls, on which 10 ribs can be counted. Growth lines are very apparent but no spiral sculpture is present. The aperture is rather narrow, semioval, and roughly occupies a little less than $\frac{2}{3}$ of the shell height. The columella is straight with 4 strong anterior plaits followed by 5 minor ones and a tooth-like projection appearing on the parietal wall below the suture. The siphonal canal is short. The basic color of the shell is a creamy yellow with spiral

chestnut lines present on the axial ribs but not visible in between. The aperture is dirty white.

Dimensions of the Shell: height, 64.0 mm; breadth, 25.5 mm; height of the aperture, 39.0 mm; breadth, 11.5 mm.

The animal has not been observed alive. Preserved in alcohol, the foot, snout and tentacles are yellowish with numerous fine, pink to red radiating lines. The sole is a uniform dirty white. Eyes are present.

Remarks: Since the monograph by WEAVER & DUPONT (1970), the descriptions of 4 more Indo-West Pacific *Lyria* have appeared:

- *Lyria taiwanica* Lan, 1975, from Taiwan, = *L. kawamurai* Habe, 1975, from Japan (WEAVER, 1977)
- *Lyria mallicki* Ladd, 1975
- *Lyria santoensis* Ladd, 1975, both from the New Hebrides Pleistocene
- *Lyria tulearensis* von Cosel & Blöcher, 1977, from Madagascar, which is apparently a local form or at most a subspecies of *L. delessertiana* (Petit de la Saussaye, 1842)

There are now 5 species of Volutidae known from the waters around New Caledonia:

- Cymbiola deshaysi* (Reeve, 1855)
- Cymbiola rossiniana* (Bernardi, 1859)
- Cymbiolacca thatcheri* (McCoy, 1868)
- Lyria deliciosa* (Montrouzier, 1859)
- Lyria kuniene* Bouchet, 1979

The name *kuniene* is derived from Kunié, the Kanak name for the Isle of Pines.

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² We have been informed that the MNHN does not assign type numbers. Editor.

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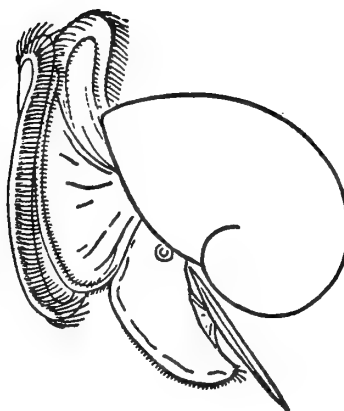




Figure 1



Figure 2

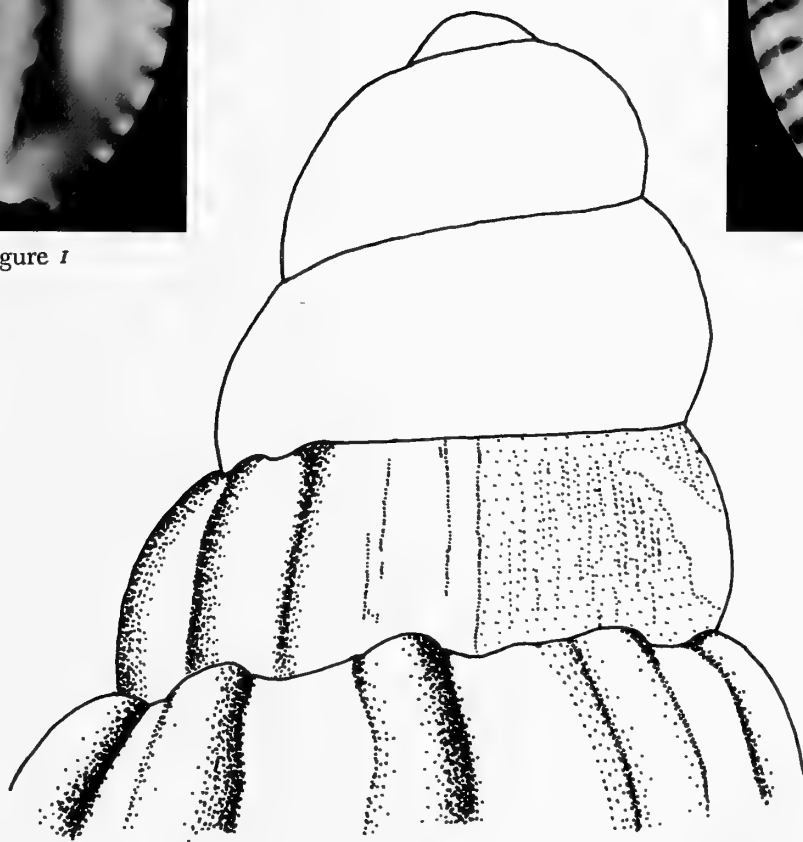


Figure 3

Lyria kuniene Bouchet, spec. nov.

Figure 1: ventral view Figure 2: dorsal view of holotype
(photographs by A. Foubert)

Figure 3: Protoconch of holotype [scale line 1 mm]

Growth and the Intertidal Gradient in the Sea Mussel

Mytilus californianus Conrad, 1837

(Mollusca : Bivalvia : Mytilidae)

BY

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(3 Text figures)

INTRODUCTION

PHENOTYPIC BIVALVE PLASTICITY has been explained in part by high and low energy environments (FOX & COE, 1943; SEED, 1968), gross percentage of time emersed (RAO, 1953; BAIRD & DRINNAN, 1957), tidal cycle (PANNELLA & MACCLINTOCK, 1968) and population density (LENT, 1967; SEED, 1968). Environmental variables themselves have been quantified, including the gross percentage of time emersed (GLYNN, 1965), single emersion period durations (DOTY, 1946) and wave impact (HARGER, 1970; RIEDL, 1971).

To my knowledge, the present study is the first in which morphological differences and the intertidal gradient are measured simultaneously. This is also the first consideration of mantle emersion response. In this study, an operational relationship between the intertidal gradient and growth in *Mytilus californianus* Conrad, 1837, is indicated. The intertidal gradient is taken to mean the continuum of change in parameters between the marine and terrestrial elements.

MATERIALS AND METHODS

Mussels were collected from December 1 to 14, 1975, at a rocky shore site north of Natural Bridges State Park, Santa Cruz, California (Figure 1). The site has nearly planar topography, with no protective outcrops. The attitude of the site (strike = N84° E, dip = 3° 20' S) is

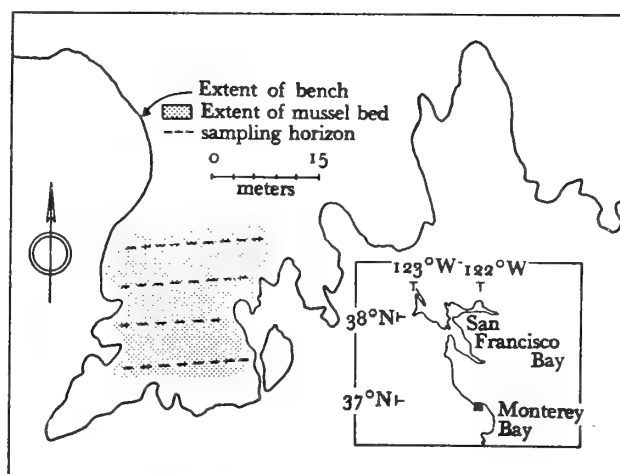


Figure 1

Map indicates location of the horizons at the study site. Inset indicates the position of the study site relative to the California coastline

such that its strike-line is parallel to the coastline of which the site is a part. Consequently, the wave fronts, which are parallel to the shore, are very nearly parallel to the strike-line of the site, yielding a more uniform wave stress at any given tidal height. Hence, site selection obviated complex patterns of wave stress and emersion duration.

Twenty samples of mussels were collected in a stratified random manner (COCHRAN, 1963; ELLIOTT, 1971; WOODIN, 1974) as follows. Four longshore lines were es-

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tablished on the mussel bed, parallel to the waterline and spaced 0.30 vertical meters apart (Figure 1). The lowest of these lines was 0.43 m above tidal datum (MLLW). Elevations were determined with a hand-held sight level and a stadia rod. The extent of mussels along these long-shore lines or "sampling horizons," varied with the shape and extent of the underlying bench of rock, which was surrounded by sand (Figure 1). Five loci were chosen within the extent of the mussels along each sampling horizon using a random number table. At each locus, a metal cylinder of 10.5 cm diameter was forced down through the mussel bed to the substrate. All mussels more than half inside, and half of those bisected by the edge of the metal cylinder were collected. Mussel density was extrapolated from this sample. The length, width, and height (Figure 2) of all mussels were measured to the

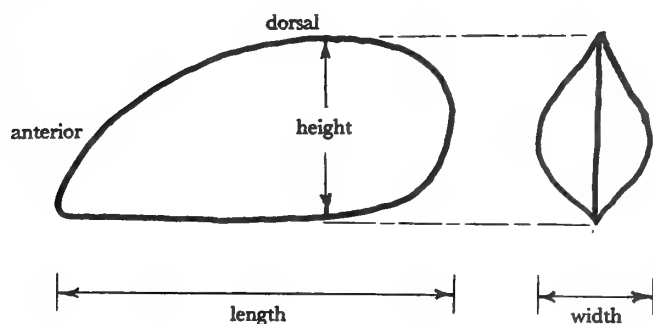


Figure 2

Definition of linear dimensions (redrawn from SEED, 1968, with permission of the Cambridge University Press)

nearest 0.1 mm. Five mussels were subsampled at random from each of the samples for weight determination. These subsamples were deemed adequate to assess trends of weight relationships based on a Monte Carlo Analysis of pilot study data. These subsamples were processed for shell weight and soft part dry weight (DAME, 1970), and visual estimates of reproductive condition were made.

After transformation to common logarithms, the data were presented as reduced major axes (RMAs) because both variables were equally subject to error (GOULD, 1966; HAYAMI & MATSUKUMA, 1970). The data were found to be validly represented (IMBRIE, 1956) by the exponential equation $y = bx^a$, where y and x are the measures of 2 parts of an individual, and b and a are empirically determined coefficients. The slopes (b) of these lines were compared with a Z-statistic based on the

standard error of estimate of the slope (*ibid.*), with tables from Mills. The number of waterline crossings (in either direction), the emersion percentages, the durations of emersed periods (DORV, 1946) for the various sampling horizons were computed from a full year (1974) of hourly tidal data recorded at Monterey, California, by the National Ocean Survey of the National Oceanic and Atmospheric Administration (NOAA). In this study, it is assumed that most of the energy from waves is transferred to the shore at the level of the waterline, and that the number of waterline crossings is an index of wave stress. Because sea and swell have no long-term correlation with the tides (W. C. Thompson, personal communication), these factors were not considered in this wave impact index derivation. Tidal fluctuations at Monterey are virtually the same as those at the study site.

Schematic representations were made from photomicrographs of the living configuration of the mantle. Ten mussels were cooled with liquid nitrogen (LN_2) to approximately $-175^\circ C$. For 5 mussels, this was done by pouring LN_2 into a container holding seawater and filtering mussels. Five closed mussels were frozen by immersion in a bath of industrial grade dichlorofluoromethane (Freon-12), which was itself immersed in LN_2 . Freon-12 has a higher boiling point than LN_2 and a melting point less than $-175^\circ C$. The Freon-12 bath was used to freeze the mantle of the closed animals quickly enough to retain their living configurations by eliminating the boiling and consequent insulation that would result from plunging the mussels directly into LN_2 . A notch was cut in the 10 frozen mussels with a surgical saw, exposing the part of a mid-abaxial section next to the ventral margin. The mussels were kept in a slurry of dry ice and acetone while photographed by reflected light at low magnification.

RESULTS

The number of waterline crossings varies directly with tidal height up to about +1 m, and varies inversely with tidal height thereafter. From these data it will be inferred that wave impact has a similar trend. Percentage of time emersed and mean duration of emersed periods vary directly with tidal height. The density of mussels is negatively correlated with tidal height of the sampling horizon where the mussels were sampled (Table 1).

The results of mussel shape and weight measurement are given in Table 2, and the results of the tests of significance, as Z-statistics and the probability that the differences arose by chance, are given in Table 3. The height-width relationship does not differ between adjacent

Table 1

Height of the sampling horizons, number of waterline crossings, percentages of time emersed, emersion durations, and population density: a waterline crossing is when the height of the waterline, in rising or falling, equals that of the sampling horizon; an emersion duration is the length, in hours, of an individual emersion, given as the mean (\bar{t}) and standard deviation (σ) of emersion duration lengths; the number of waterline crossings, percentages of time emersed and emersion durations are based on a 1-year study.

Height of sampling horizon m from MLLW	Number of waterline crossings	Percentage of time emersed	Emersion duration h		Density, mussels/m ²
			\bar{t}	σ	
+1.34	758	83	16.8	5.3	9700
+1.04	1286	59	8.2	3.6	12200
+0.73	1072	35	5.7	1.5	16200
+0.43	792	20	4.5	1.5	16200

samples, but there are differences between non-adjacent samples. The height-length relationships increase with the tidal height of the samples. Considering mussels from the lower 2 sampling horizons as one relation, there is a direct correlation between sampling horizon height and the

width of the mussels with respect to length. None of the shell height-length slopes differ significantly. Mussels from the 2 higher sampling horizons have heavier shells, with respect to length, than mussels from the 2 lower sampling horizons. Mussels from the highest sampling horizon have

Table 2

Slope coefficients and Y-intercept coefficients of reduced major axes, r^2 values, and the number of mussels in the sample from which the reduced major axes were derived: the information is given in the above order in each data block.

Relationship, y/x	+0.43	+0.73	+1.04	+1.34
Width/Length	0.992 \pm 0.009	0.996 \pm 0.008	1.057 \pm 0.022	1.131 \pm 0.020
	-0.435	-0.433	-0.481	-0.560
	0.988	0.984	0.955	0.973
	142	126	106	84
Height/Length	0.867 \pm 0.010	0.841 \pm 0.012	0.839 \pm 0.018	0.864 \pm 0.016
	-0.082	-0.047	-0.040	-0.063
	0.980	0.975	0.952	0.972
	142	126	106	84
Height/Width	0.874 \pm 0.013	0.844 \pm 0.014	0.794 \pm 0.022	0.764 \pm 0.016
	0.298	0.319	0.342	0.364
	0.966	0.964	0.919	0.962
	142	126	106	84
Shell Weight/Length	2.766 \pm 0.037	2.717 \pm 0.058	2.969 \pm 0.062	3.082 \pm 0.073
	-3.982	-3.788	-4.142	-4.213
	0.995	0.989	0.989	0.986
	25	25	25	25
Tissue Weight/Shell Weight	1.070 \pm 0.012	1.053 \pm 0.011	0.978 \pm 0.019	1.013 \pm 0.024
	-1.006	-1.030	-1.076	-1.131
	0.997	0.997	0.990	0.986
	25	25	25	25

Table 3

Results of the tests of significance, as Z-statistics and the probability that the difference between the samples arose by chance, all possible comparisons were made for each relationship: the information is given in the above order in each data block.

Relationship, y/x	+0.43, +0.73	+0.43, +1.04	+0.43, +1.34	+0.73, +1.04	+0.73, +1.34	+1.04, +1.34
Width/ Length	0.34 <0.70	-2.74 <0.01	-6.25 ≤0.0001	-2.62 <0.01	-6.21 ≤0.0001	-2.49 <0.02
Height/ Length	1.69 <0.10	1.34 <0.20	0.13 >0.90	0.06 >0.90	-1.21 >0.30	-1.06 >0.30
Height/ Width	1.54 >0.10	3.09 <0.002	5.20 ≤0.0001	1.90 >0.05	3.70 <0.001	1.09 >0.30
Shell Weight/ Length	0.72 >0.50	-2.97 <0.01	-2.79 <0.001	-3.93 <0.001	-3.86 <0.001	-1.19 <0.30
Tissue Weight/ Shell Weight	1.04 >0.30	4.02 <0.001	2.11 <0.05	3.34 <0.01	1.51 >0.05	-1.14 >0.05

heavier shells, with respect to soft part weight, than mussels from the lowest sampling horizon. Mussels from the +1.04 m sampling horizon have heavier shells than those from the 2 lower sampling horizons.

The RMAs of the height-width, width-length, shell weight-length, and soft part weight-shell weight plots differ more in slope than in Y-intercept (as evident in the appearance of the plotted data). The RMAs of the shell-height plots differ neither in slope nor Y-intercept.

In animals frozen while immersed with open valves, the edge of the outer (secretory) mantle fold was found to be even with, or slightly outside the shell margin (Figure 3). In animals frozen while emerged with closed valves, the edge of the outer fold was withdrawn within the shell margin.

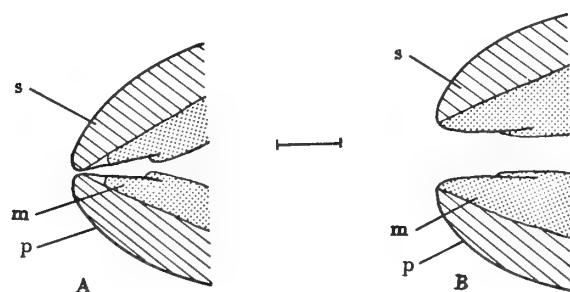


Figure 3

Schematic representation of mid-abaxial sections of mussel ventrum. (A) mussel with shell closed (animal emerged) (B) mussel with shell open (animal immersed). m - mantle s - shell p - periostracum

DISCUSSION

A brief, general look at the data yields the following correlations. Abiotic parameters, as a whole increasing with the tidal height of the samples, can explain the similar general mussel shape and weight trend. Emersion percentage or duration, or both, alone could also explain the shape and weight data trend, as these 2 sets of data vary together. However, wave stress alone cannot cause the shape and weight trends, because it is discontinuous. Further, a discontinuity resembling that of the wave stress data is not found in the shape and weight data. The results also establish the possibility of some causative role for population density.

Mantle retraction in response to stress (SEED, 1968; PANNELLA & MACCLINTOCK, 1968; present study) likely effects shell growth more toward the midline and less in height and length (SEED, 1968). Thus the relative increased width in this study's high-shore animals can be related to the relatively greater amount of their life-cycles spent emersed. This also concurs with the contention that "normal" outer shell deposition can occur only with open valves and subsequent mantle extension well along the margins (PANNELLA & MACCLINTOCK, *op. cit.*). Study of short-term accretion in stressed and unstressed *Mytilus californianus*, as was done with *Mercenaria mercenaria* (Linnaeus) (*ibid.*) would help to understand this process, although these studies would be more difficult with the reflected margin of *M. californianus*.

Support for a direct, causal connection between emersion time and shell growth patterns is found in studies of

species differing in their emersion responses. Shell shape changes with tidal height (*Mytilus californianus*: FOX & COE, 1943; present study; *Mytilus edulis* Linnaeus, 1758: SEED, 1968) have been found in species where valve closure always or almost always accompanies emersion (*M. californianus*: personal observation; *M. edulis*: COLEMAN, 1973) whereas no such shell shape changes were found (LENT, 1967) in *Modiolus demissus* Dillwyn, 1817, which air-gapes excessively (COLEMAN, *op. cit.*). Evidence that shell growth during closure is greatly retarded but continues (PANNELLA & MACCLINTOCK, 1968) or is net positive in spite of interim dissolution (BAIRD & DRINNAN, 1957) seems to leave open the possibility of modest width accretion during closure, especially when growth in height and length are likely even slower during closure.

Wide mussels high on the shore are equally explicable by having growth in height and length attenuated either ontogenetically (SEED, 1968), or by a longer time spent emersed (this report). Data from old mussels found low on the shore would seem to offer arbitration between these two explanations. The rarity of such animals has been attributed to the effect of the feeding patterns of desiccation-intolerant predators (*Mytilus edulis*: SEED, 1968; *M. californianus*: PAINE, 1976). Even in the absence of predation, however, the survival of *M. edulis* in the Menai Straits, North Wales, has been found to be markedly poorer at the 2% (spring extreme low water) exposure level than at the 6-20% exposure levels (P. J. Dare & G. Davies, unpublished data). Hence a search for arbitration in the form of old mussels from low on the shore may be fruitless, and therefore contraindicated. In either case, the result of allometric growth would be enhanced by a high shore shift toward longer-lived animals (*M. edulis*: SEED, *op. cit.*; *M. californianus*: PAINE, *op. cit.*), as the difference would accumulate with time.

If population density (FOX & COE, 1943; LENT, 1967; SEED, 1968) or overall growth rate (COE & FOX, 1942; COE, 1945) were each the sole or primary cause of shell shape changes with tidal height, we may well predict that mussels either show a simultaneous diminution of height and width relative to length with increasing population density, or changes in shell size alone with no shell shape changes, respectively. The former prediction is based on the assumption by animals of an orientation with long axes normal to the substrate in high population densities (LENT, 1967; SEED, *op. cit.*; present study). The trend of height relative to width, in addition to the independent comparisons of height relative to length, and width relative to length, deny strict realization of these expectations. However, mussel girth (height and width

taken together) does in fact decrease with an increase in population density, thereby leaving open the possibility of some causal link between these parameters.

Wave impact may cause thickened shells (COE & FOX, 1942), but the wave data reported here eliminate wave stress as the sole cause of the trend of shell weight relative to length. However, shell width (*ibid.*; present study) correlates well with shell weight relative to length, and could be the cause of the weight trend, when it is considered that a wider mussel of a given length and height is likely to be heavier. Whether wave stress and emersion act in concert or separately on shell thickness and width is unknown. Study of mantle position under wave stress would certainly help arbitrate putative causal links between these parameters.

Growth in height and length are equally affected by, and hence exhibit no relative variance along the emersion gradient. This results naturally from the relationship between the emersion-affected mantle position and shell growth advanced in this study, because accretion to both height and length occurs when the mantle is protracted, and little or no accretion occurs to either when the mantle is retracted.

Efforts to measure the tissue/shell weight relationship, a crucial gross energetic parameter, are plagued with problems. The trend revealed in this study (also in BAIRD & DRINNAN, 1957; LENT, 1966; SEED, 1973) is opposite to RAO's (1953) results. Rao discarded all "gravid" animals, possibly biasing his samples toward juveniles. This bias can give high shell/tissue weight ratios (SEED, *op. cit.*). Further complications arise from indiscrete, disagreed upon or even year-round spawning in *Mytilus californianus* (*ibid.*), with *M. edulis* giving a 100% annual tissue weight variance (DARE & EDWARDS, 1975). Future studies may do well to include averages of year-round collections (FOX & COE, 1943).

An interesting contradiction has arisen between the results of various studies of mussels. Allometric plots that vary more, judging from the visual appearance of the plots, in slope than Y-intercept (*Mytilus californianus*: FOX & COE, 1943; present study; *M. edulis*: SEED, 1968, 1973) usually represent phenotypically different, genotypically similar samples, while those varying more in Y-intercept than slope represent genotypic variance (GOULD, 1966). Thus the former type of variance is the accumulating effect through time of differing environmental regimes (SEED, 1968). However, several workers report inter-site (*M. californianus*), and inter- and intra-site (*M. edulis*) genetic variance via enzyme electrophoresis (LEVINTON & KOEHN, 1976). This apparent contradiction awaits resolution.

SUMMARY

1. *Mytilus californianus* were sampled in a random stratified fashion from the California rocky intertidal zone.
2. Shell width and weight relative to length and shell width relative to height had a positive and significant correlation, tissue weight relative to shell weight had a negative and significant correlation, and shell height relative to length had no correlation with tidal height.
3. Emersion percentage time and average emersion duration had a positive correlation, wave impact had a partial positive correlation, and population density had a negative correlation with tidal height.
4. Cryogenic preparations reveal a retracted outer mantle fold during emersion. This is used to explain change in shell shape with the emersion differential.
5. The findings of this report are compatible with explanations elsewhere of spatial demographic shift and partial ontogenetic attenuation of growth, but are in conflict with explanations involving population density, overall growth rate, and wave stress.
6. Year-round collection is recommended for tissue-shell weight ratio determination.
7. Genotypic variance findings in this report conflict with recent biochemical studies elsewhere.

ACKNOWLEDGMENTS

For guidance and assistance, I would like to thank my colleagues at the University of California, Santa Cruz, especially Drs. M. W. Silver, A. T. Newberry, and J. S. Pearse. Also, my sincere thanks to W. C. Thompson, U. S. Naval Postgraduate School, Monterey, California, for providing the NOAA data and advice; to Drs. D. L. Fox, Scripps Institution of Oceanography, R. Seed, University College of North Wales, J. J. Gonor, Oregon State University, and W. Lee, California Academy of Sciences, for critical review of the manuscript; and to P. J. Dare and G. Davies, Ministry of Agriculture, Fisheries and Food, Conwy, Wales, for gracious provision of unpublished data. Illustrations are by G. M. Breed, O. S. U. S. D. G.

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Problacmaea moskalevi Golikov & Kussakin,
a New Addition to the Eastern Pacific Limpet Fauna

(Archaeogastropoda : Acmaeidae)

BY

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(2 Plates; 3 Text figures)

THE ACMAEID GENUS *Problacmaea* Golikov & Kussakin, 1972, is represented by 2 extant species in the boreal Pacific: *Problacmaea sybaritica* (Dall, 1871) and *P. moskalevi* Golikov & Kussakin, 1972. Members of the genus differ from other acmaeids in possessing a penis-like structure under the right cephalic tentacle. The radula is typical of species that feed on encrusting algae, having 3 lateral teeth approximately equal in size and shape and arranged in a chevron-like pattern. The shells are white or reddish with or without darker rays, and are sculptured with concentric growth lines and in some, radial riblets.

Problacmaea sybaritica has an extensive distribution in the northern Pacific: Hakodate, Japan (43°N, 141°E), Plover Bay, Chukotskiy Polvostrov, U. S. S. R. (64°N, 173°W), Pribilof Islands (57°N, 170°W), Aleutian Islands to Chirikof Island, Alaska (56°N, 156°W) (McLean, 1966: 47), but the type of the genus, *P. moskalevi*, has been previously reported only from localities in the seas of Okhotsk and Japan, U. S. S. R. Recently, Dr. James H. McLean, Los Angeles County Museum of Natural History (LACM), noted that a specimen lot of *Lepeta concentrica* (Middendorff, 1847) from Alaska contained a single specimen that was different; it had smaller limpets attached to its dried body. Dr. McLean brought this specimen to my attention, and after examining it I have identified it as *P. moskalevi*.

The specimen, re-catalogued as United States National Museum of Natural History (USNM) No. 749078, was collected on stones at a depth of 6.5 m in Amkagnak Straits, Captain's Bay, Unalaska, Aleutian Islands, Alaska (53°52'N, 166°34'W) by W. H. Dall in the early 1870's.

This represents a new distributional record over 2500 km east of the previous localities and suggests that this species may be present throughout the Aleutian Island arc. It is ironic that Dall, who contributed so extensively to acmaeid systematics and anatomy, overlooked this unique specimen, and thus it remained undescribed for approximately 100 years.

The original description of *Problacmaea moskalevi*, translated from French, is given here and followed with additional remarks based on the Dall specimen.

Problacmaea moskalevi

"The shell is fine, rather fragile with a rounded oval base and a raised subcentral apex. The shell is white. The sculpture is described simply as concentric growth lines set off by annual rings. The inner surface of the shell has a small grey spot near the apex. The radula is typical of the genus. Height of the holotype: 4.7 mm, length 10.5 mm, width 9.5 mm. Type locality— shallow basin in the middle horizon of the mesolittoral at Ostrov Bol'shoy Shantar [55°N, 137°42'E], Sea of Okhotsk (collected by M. B. Ivanova, 10 October 1966). The holotype is deposited in the systematic collections of the Institute of Zoology, Academy of Sciences of the U. S. S. R. [Leningrad]. The species is named in honor of Dr. L. Moskalev, a well-known specialist in limpets." (GOLIKOV & KUSSAKIN, 1972: 290)

Golikov & Kussakin compared *Problacmaea moskalevi*

to *Acmaea apicina* Dall, 1879, noting that the 2 species were superficially similar but differed in their respective length/height and width/height ratios, *P. moskalevi* being consistently lower than *A. apicina*. Also, they considered *P. moskalevi*, like *P. sybaritica*, to be ovoviviparous and a protandric hermaphrodite. A paratype *P. moskalevi* from the type locality contained a large number of embryos with shells in its nuchal cavity. The embryonic shells were approximately 0.3 mm in length. Other specimens from Tartarskiy Proliv, Sea of Japan (50°N, 141°E), collected at a depth of 35 - 37 m from sand and mud substrata, had nuchal cavities filled with large eggs, approximately 0.115

mm in diameter. Golikov & Kussakin examined all together 11 specimens of *P. moskalevi* from 3 localities.¹

The Dall specimen (Figure 1) is 6.6 mm in length, 5.7 mm in width, and 2.8 mm in height. The length/height ratio is 2.4; the width/height ratio 2.0, both being slightly greater (+0.1) than the ratios given by Golikov & Kussakin for Asiatic specimens of *Problacmaea moskalevi*. The shell is white and encrusted with coralline algae. The anterior slope is slightly concave, the apex anteriorly directed. The posterior slope is convex and the lateral slopes straight. Sculpture of concentric growth lines is visible only at the shell margin. Viewed in profile the shell shows

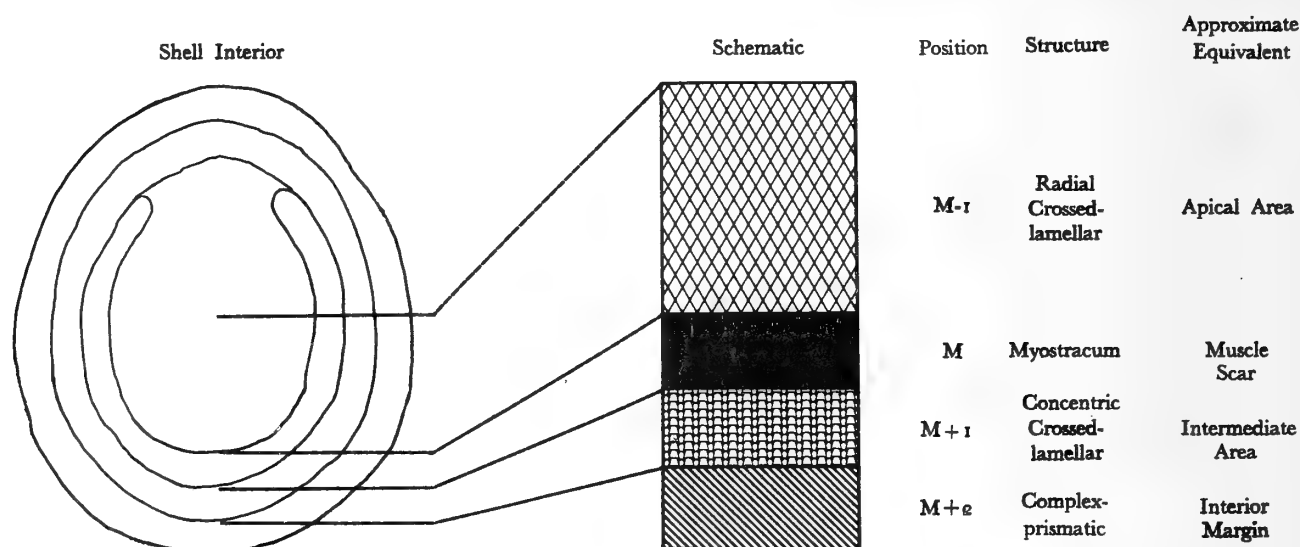


Figure 2

¹ Additional localities represented in Golikov and Kussakin's material are: Simushir (46°58'N, 152°02'E), Urup (46°N, 150°E) and Iturup (44°54'N, 147°30'E), Kuril Skiye Ostrova, U. S. S. R.; 5 - 15 m on sand and stones (A. N. Golikov, *in litt.* March, 1978)

Shell structure of the genus *Problacmaea* illustrating relationship of structure groups to terms used in acmaeid systematics. M - myostracum; m-1 - first structure group interior of myostracum; m+1 - first structure group exterior of myostracum, etc.

Explanation of Figures 1a to 1c, 4 to 8

Figure 1: *Problacmaea moskalevi* Golikov & Kussakin, 1972. ALASKA: Aleutian Islands, Unalaska (USNM No. 749078); shell length: 6.6 mm a - dorsal; b - ventral; c - profile
Figure 4: Dried body of *Problacmaea moskalevi* (USNM No. 749078). Body length: 3.9 mm. NC - remnant of nuchal cavity containing young limpets; V - viscera; IL - intestinal loops
Figures 5 to 8: Protoconch of *Problacmaea moskalevi* (USNM No. 749078). Figure 5: dorsal view, × 340; Figure 6: anterior view, × 300; Figure 7: lateral view, × 340; Figure 8: posterior view, × 290



Figure 1a

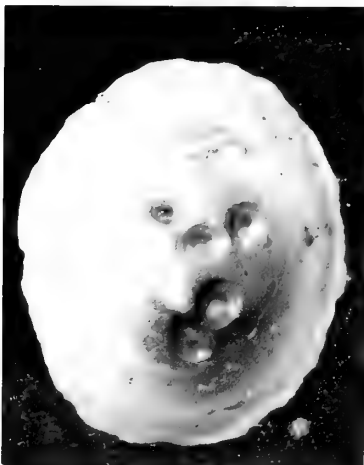


Figure 1b



Figure 4

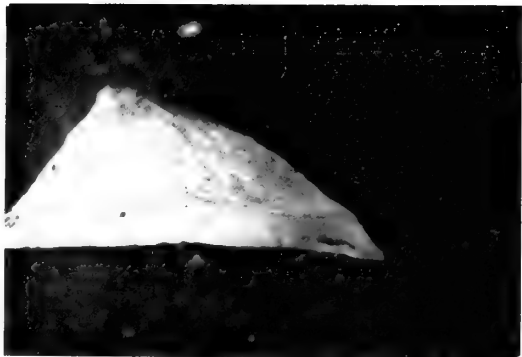


Figure 1c

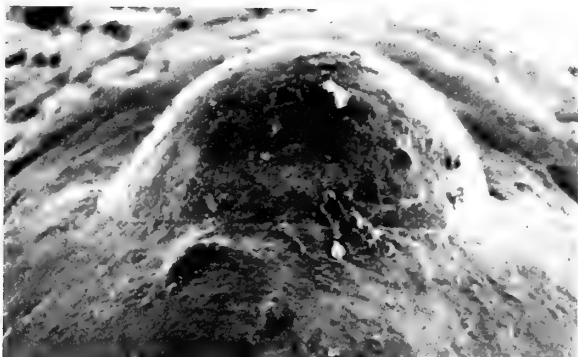


Figure 6

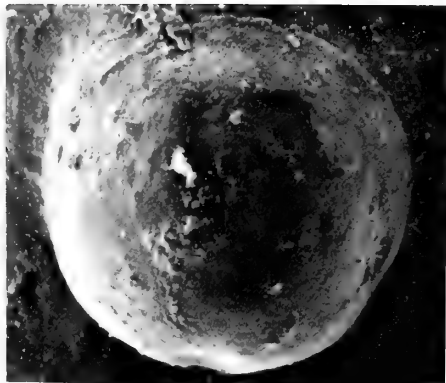


Figure 5

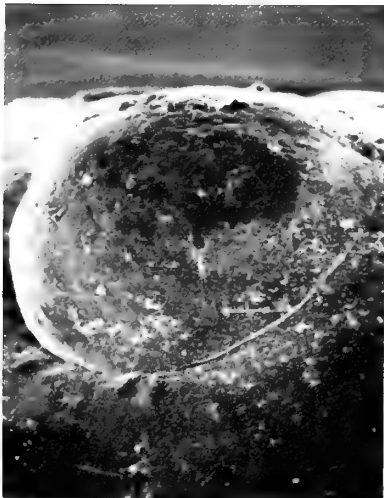


Figure 7



Figure 8

unequal growth increments that result in uneven slopes [= Golikov & Kussakin's "annual rings"?]. The interior is whitish with a slight yellow cast near the margin. The apical area is covered by the dried mantle, to which several young limpets are attached. The gray spot mentioned by Golikov & Kussakin, if present, is not visible through the dried mantle. The shell structure (Figure 2), determined from the concentric bands visible on the inner surface, appears to be identical to that of *P. sybaritica*, except that the inner margin (complex prismatic layer) of *P. moskalevi* is much narrower than in *P. sybaritica*. The radula of the Dall specimen was not examined. Golikov & Kussakin's figure of the radula of *P. moskalevi* is given here in Figure 3.

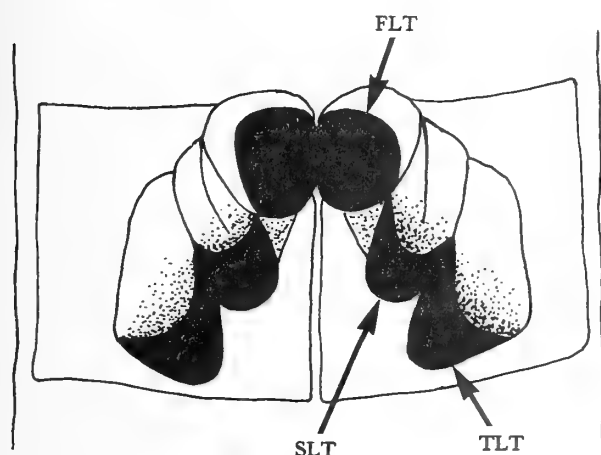


Figure 3

Radula of *Probalacmaea moskalevi* (redrawn from GOLIKOV & KUSSAKIN, 1972). FLT - first lateral teeth; SLT - second lateral teeth; TLT - third lateral teeth; scale unknown

The dried body of the specimen (Figure 4) is 3.9 mm in length and contains 24 small limpets in the nuchal cavity. Although contracted, large oral lappets are visible on the muzzle. The foot is remarkably small, approximately 1.5 mm in length. The nuchal cavity is large, approximately 3.3 mm in length or almost 85% of the animal's total length. Neither the ctenidium nor the nephridiopores are visible because the specimen is dried and shriveled and the region is obscured by the juvenile limpets in the nuchal cavity. The visceral area is markedly posterior and ventral; the intestinal loops contain a whitish material that appears to be calcium carbonate. The penis-like structure is not visible under the right cephalic tentacle. I do not know whether this is due to the specimen's dried

and contracted state, atrophy of the structure accompanying sex change, or degrees of both.

Based upon the embryonic shells in the Dall specimen, the protoconch of *Probalacmaea moskalevi* (Figures 5-8) is positioned in the center of the teleoconch (Figure 9). There is a slight asymmetry, the posterior portion of the protoconch being slightly to the left of the longitudinal axis of the teleoconch. The lateral edges of the protoconch are straight and approximately parallel. The posterior portion is rounded, with a small indentation on the postero-dorsal surface. The surface appears smooth, with no sculpturing. No coiling is visible, and the protoconch is presumed to be caecum-like. The posterior slope is strongly convex and ventrally appressed to the teleoconch (Figures 7-8). The anterior slope is also convex although not as strongly as the posterior (Figure 7). The entire protoconch is separated from the teleoconch by a fine suture (Figure 5). The initial teleoconch lacks sculpture and forms a slight depression around the posterior and lateral margins of the protoconch (Figure 8). After the initial growth, the teleoconch is sculptured with approximately 40 sinuous, flat topped ribs (Figure 9). The interspaces between the ribs are divided by numerous ridges (Figure 10). Nearer the margin these ribs disappear, and the strong concentric growth lines typical of the species become apparent (Figure 11).

DISCUSSION

The shell structure of *Probalacmaea* is identical to that of the western Pacific genus *Patelloida* Quoy & Gaimard, 1834, and unlike that of *Acmaea*, *Collisella*, and *Notoacmaea* (MACCLINTOCK, 1967). Although the genus *Patelloida* is characterized by 2 pairs of radular marginal teeth, the genus *Probalacmaea* is simply derived by the loss of the marginal teeth as the radula became modified for feeding on encrusting algae. I consider the similarity of shell and radular morphologies to members of the eastern Pacific genus *Acmaea* Eschscholtz, 1833, to result from convergence rather than common ancestry.

In temperate and tropical species acmaeid reproductive strategy consists of external fertilization and pelagic development. THORSON (1950) has shown that Arctic and near-Arctic prosobranchs tend to delete the pelagic phase and instead brood their young. In view of this model the apparent departure from typical acmaeid reproductive strategy by members of the genus *Probalacmaea* is not surprising, and it is unlikely that this represents a distinct evolutionary tendency within the Acmaeidae worthy of subfamilial rank as proposed by GOLIKOV & KUSSAKIN (1972: 292).

The protoconch of *Problacmaea moskalevi* is similar to that of *P. sybaritica* (Figures 12, 13). The lateral pouches (Figure 14) described and figured by MORSE (1910) and THOMPSON (1912) in eastern Pacific and western Atlantic acmaeids are not present in either species of *Problacmaea*. Instead there is a simple suture between the apex and the lip of the protoconch of *P. sybaritica* that is

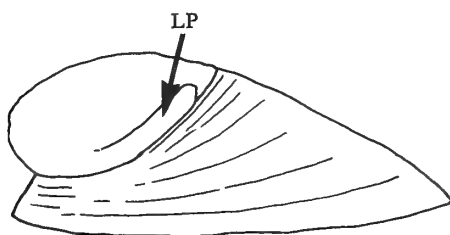


Figure 14

Protoconch of *Acmaea* sp. (redrawn from MORSE, 1910).
LP - lateral pouches; scale unknown

visible under high illumination light microscopy. A ridge is also visible through the protoconch that seems to connect the anterior ends of the sutures. These sutures are not visible in the protoconchs of *P. moskalevi*, presumably because of the more advanced stage of development of these shells, the ventral portion of the protoconch being overlapped by the teleoconch. Specimens observed at an earlier stage of development would most likely show these sutures.

The early teleoconch of *Problacmaea moskalevi* most closely resembles that of the Arctic species *Acmaea rubella* (Fabricius, 1780) (cf. THORSON, 1935: 68; fig. 74), both species being sculptured with distinct radial riblets on the early teleoconch but having only concentric growth lines as adults. Specimens of *P. sybaritica* collected by McLean in 1973 show that the initial teleoconch of *P.*

sybaritica is smooth but soon develops pits similar to those in *P. moskalevi*. Because of the early stage of development of these shells I can not determine if these pits give rise to radial riblets as they do in *P. moskalevi*. However, as *P. sybaritica* is sculptured with fine radial riblets as an adult, I suspect that this is the case.

ACKNOWLEDGMENTS

I wish to thank Dr. James H. McLean (LACM) for bringing the specimen of *Problacmaea moskalevi* to my attention, and also kindly reviewing the manuscript. Dr. Joseph Rosewater (USNM) supplied additional locality data on the Dall specimen. Dr. Alexandre N. Golikov (Academy of Sciences, Leningrad) supplied additional locality data on the western Pacific specimens. Special thanks to Ms. Jan Nowell (University of California Santa Cruz) for her assistance and patience with the scanning electron microscopy portion of this study.

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Explanation of Figures 9 to 13

Figures 9 to 11: Early teleoconch of *Problacmaea moskalevi* (US NM No. 749078), shell length 0.9 mm. Figure 9: dorsal view, $\times 80$; Figure 10: radial sculpture, $\times 660$; Figure 11: interface of radial sculpture with adult sculpturing, $\times 660$

Figures 12 and 13: Protoconch and early teleoconch of *Problacmaea sybaritica* (Dall, 1871). ALASKA: Kenai Peninsula, Seldovia Bay (LACM No. 73-18). Shell length 0.6 mm. Figure 12: dorsal view, $\times 275$; Figure 13: lateral view, $\times 230$



Figure 9

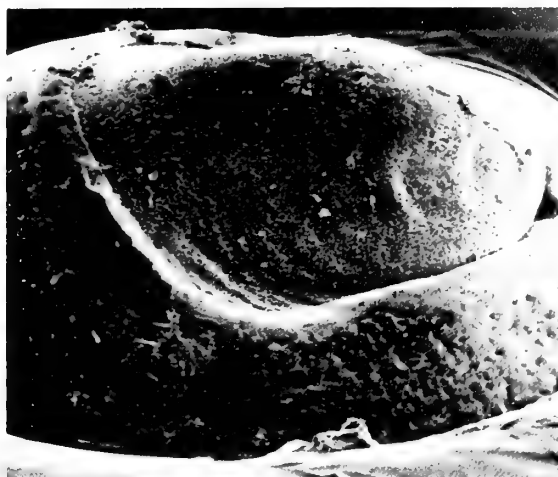


Figure 13

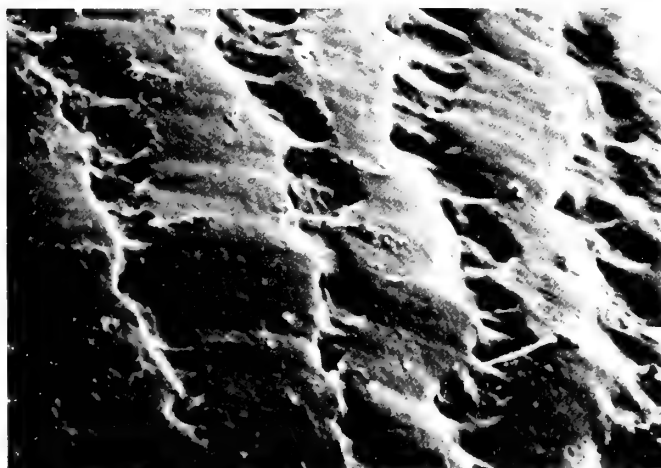


Figure 10



Figure 12

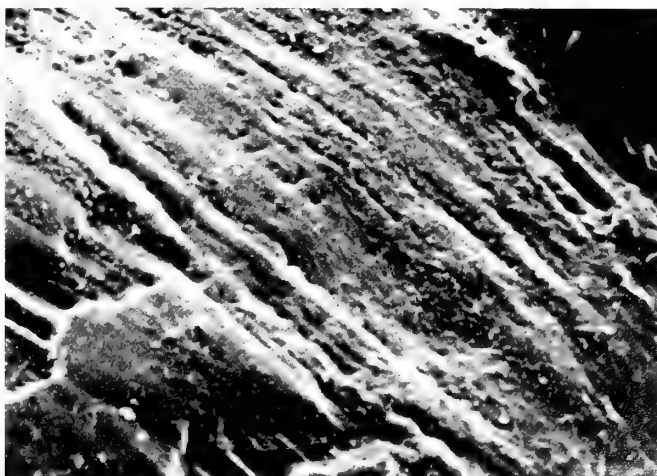


Figure 11

Taxonomic Changes in Eastern Pacific Terebridae, with the Description of a New Species

(Mollusca : Gastropoda)

BY

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(1 Plate)

INTRODUCTION

FURTHER WORK on the eastern Pacific Terebridae since the publication of the second edition of Dr. Keen's "Seashells of Tropical West America" has produced a number of changes. Re-examination of the type specimens, after my becoming more thoroughly familiar with eastern Pacific terebrid fauna, cleared up a problem concerning *Terebra elata* Hinds, 1844. The 2 forms illustrated as *T. elata* by BRATCHER & BURCH in KEEN (1971) actually prove to be separate species. The true *T. elata* Hinds is the smaller, more finely sculptured one. The larger, more coarsely sculptured one is *T. guayaquilensis* E. A. Smith, 1880.

Work with the type specimens in the British Museum (Natural History) also brought the discovery that *Terebra glauca* Hinds, 1844, has been misidentified. *Terebra dorothyae* Bratcher & Burch, 1970, is a synonym of the true *T. glauca*. The name *T. petiveriana* Deshayes, 1857, must be applied to the species formerly identified as *T. glauca* of authors and illustrated as such in both editions of Keen's "Seashells of Tropical West America."

TEREBRIDAE Mörch, 1852

Terebra Bruguière, 1789

Terebra elata Hinds, 1844

(Figure 1)

Terebra elata HINDS, 1844: 156 [not figured]; HINDS, 1845: 177, plt. 44, figs. 68-69; CATLOW & REEVE, 1845: 289; C. B. ADAMS, 1852: 45; REEVE, 1860: sp. 128, plt. 24;

GRANT & GALE, 1931: 470; KEEN, 1958: 491, fig. 962 [left fig. only]; KEEN, 1966: 273, plt. 47, fig. 14; BRATCHER & BURCH in KEEN, 1971: 674, fig. 1535 [right fig. only]

Description of Species: Shell moderately small, to 25 mm, slender; color white or pale beige, occasionally with a few yellow blotches; outline of whorls convex, with convex subsutural band; protoconch multispiral, consisting of $3\frac{1}{2}$ smooth, glassy conoidal embryonic whorls; early whorls of teleoconch sculptured with many fine, sharp, slightly curved ribs, narrower than interspaces, containing about 5 spiral grooves not crossing axial ribs; subsutural groove appearing at about 4th whorl of teleoconch; later whorls sculptured with curved ribs narrower than interspaces, 16 to 20 on body whorl; spiral grooves, 4 to 8, sometimes crossing axial ribs, giving a slightly beaded appearance; spiral and axial sculpture sometimes continuing anterior to periphery of body whorl but not always constant; outer lip thin; aperture moderately elongate; columella recurved with simple basal fold; siphonal fasciole striate with sharp keel.

Type Locality: Bay of Montijo, west coast of America, in 15 fathoms [27 m], coarse sand.

Type Specimens: Holotype, British Museum (Natural History) no. 1968240

Discussion: The first several whorls of the teleoconch and area anterior to the periphery of the body whorl are often purple in fresh specimens. The purple usually fades to a brownish color.

Terebra elata is a more slender and more delicate shell than *T. guayaquilensis* and the whorls are less convex.

Terebra guayaquilensis E. A. Smith, 1880

(Figure 2)

Terebra belcheri E. A. SMITH, 1873: 267 [non PHILIPPI, 1852]*Terebra guayaquilensis* E. A. SMITH, 1880: 481*Terebra ira* PILSBRY & LOWE, 1932: 40, plt. 1, fig. 13; KEEN, 1958: 492, fig. 966*Terebra elata* Hinds, BRATCHER & BURCH in KEEN, 1971: 676, fig. 1635 [left fig. only]

Description of Species: Size medium to 41 mm; base color white to beige, often with yellowish blotches or bands; outline of whorls convex, with convex subsutural band; protoconch of $1\frac{1}{2}$ smooth, glassy, embryonic whorls; sculpture of early whorls of teleoconch of many fine, sharp, slightly curved axial ribs narrower than interspaces, containing about 5 spiral grooves that may or may not faintly cross ribs; groove marking subsutural band appearing at about 4th whorl of teleoconch; sculpture of later whorls extremely variable, some individuals having strong wide-spaced spiral grooves, as few as 3 per whorl, not overriding ribs, others having as many as 5 heavy spiral cords, overriding ribs to form small beads at intersections; ribs sometimes close-set in early whorls, usually becoming wide-spaced later; sutures deep, with subsutural groove usually cutting through axial ribs; axial sculpture of body whorl fading at periphery in some individuals; spiral sculpture continuing to anterior of shell; aperture semiquadrate; columella recurved, with faint basal fold; siphonal fasciole striate, with sharp keel.

Type Locality: Guayaquil, Ecuador.**Type Specimen:** Holotype, British Museum (Natural History) no. 44.6.7.77, length 38.0 mm

Discussion: A very young specimen of this species could be easily confused with *Terebra elata* Hinds, as the early sculpture is fine; both species have similar protoconchs and about the same apical angle. *Terebra guaya-*

quilensis has not been observed with the purple early whorls of the teleoconch that occurs in many specimens of *T. elata*. *Terebra guayaquilensis* becomes a larger shell in its maturity and develops much coarser and more variable sculpture in its later whorls. *Terebra elata* has a shinier shell.

Terebra glauca Hinds, 1844

(Figure 3)

Terebra glauca HINDS, 1844: 155 [not figured]; HINDS, 1845:

175, plt. 44, fig. 85; KEEN, 1966: 273, plt. 47, fig. 16

Terebra dorotheae BRATCHER & BURCH, 1970: 297, plt. 44, figs. 7-8; BRATCHER & BURCH in KEEN, 1971: 676, fig. 1534

Description of Species: Size medium, to 36 mm; color brown, portions of subsutural band and nodes slightly lighter; outline of whorls with early whorls being somewhat convex and later whorls almost flat, with moderately convex subsutural band; protoconch multispiral, of 3 slender, glassy whorls, the first 2 usually light brown in color; early whorls of teleoconch with ribs extending from node on subsutural band to following suture; nodes on band becoming elongate on later whorls; ribs on remainder of whorl broken into nodes by spiral bands, body whorl with spiral rows of nodes to periphery; aperture elongate; outer lip thin, with pattern of nodes and sometimes a light peripheral band showing through; columella slightly curved, with no plication; siphonal fasciole heavy, striated, posterior keel exceptionally large.

Type Locality: Unknown**Type Specimen:** Holotype, British Museum (Natural History)

Discussion: *Terebra glauca* has a monochromatic shell with nodes and portions of the subsutural band slightly

Explanation of Figures 1 to 12

Figure 1: *Terebra elata* Hinds, 1844. Holotype, BM[NH] no. 1968420Figure 2: *Terebra guayaquilensis* E. A. Smith, 1880 nom. nov. pro *Myurella belcheri* E. A. Smith, 1873 [non *Terebra belcheri* Philippi, 1851] Holotype, BM[NH] no. 44.6.7.77Figure 3: *Terebra glauca* Hinds, 1844. Holotype BM[NH]Figure 4: *Terebra petiveriana* Deshayes, 1857. Holotype BM[NH]Figure 5: *Terebra carolae* Bratcher, spec. nov. Holotype LACM-AHF no. 1178Figure 6: *Terebra variegata* Gray, 1834. Bratcher collectionFigure 7: *Terebra carolae*. Same specimen as in Figure 5Figure 8: *Terebra variegata*, aperture. Bratcher collectionFigure 9: *Terebra carolae*, interior columella. Bratcher collectionFigure 10: *Terebra variegata*, interior columella. Bratcher collect.Figure 11: *Terebra carolae*, protoconch. Paratype, LACM-AHF no. 1184Figure 12: *Terebra variegata*, protoconch. Bratcher collection



Figure 1

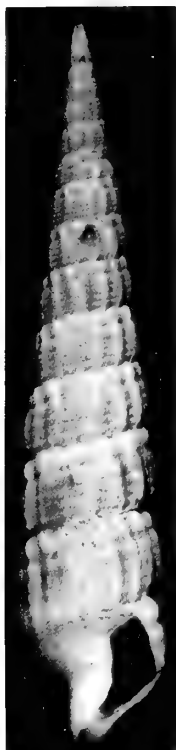


Figure 2



Figure 3

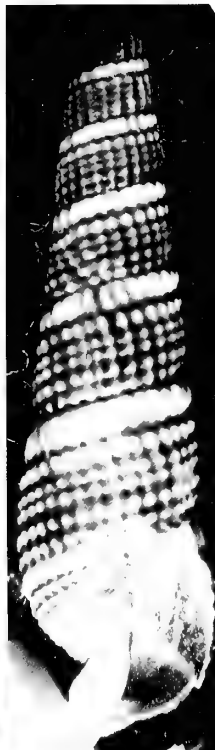


Figure 4

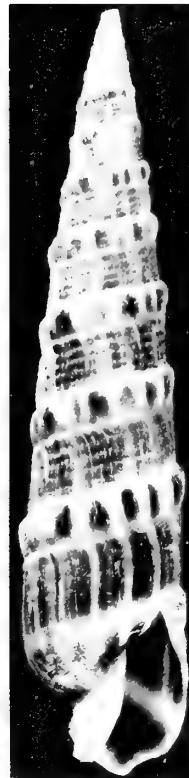


Figure 5



Figure 6

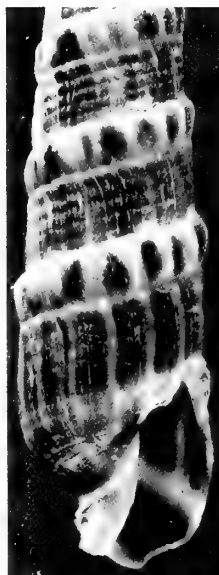


Figure 7



Figure 8



Figure 9



Figure 10



Figure 11



Figure 12

lighter in intensity of color. The sculpture is of definite nodes. The shell is thin and delicate. *Terebra petiveriana* Deshayes has a thicker subsutural band, usually of a definite contrast in color. Though often noded, frequently the sculpture is of rough axial ribs. Its shell is heavier and broader with coarser sculpture and with 2 folds on the columella.

Although there appear to be 2 syntypes of *Terebra glauca* in the British Museum type collection, the word "unique" on the back of the mount seems to imply that originally there was only 1 specimen, the other being added later. The larger, more centrally mounted specimen closely matches Hind's measurements, so it must be considered the holotype.

Terebra petiveriana Deshayes, 1857

(Figure 4)

Terebra aspera HINDS, 1844: 154 [non BOSC, 1801] [not figured]; HINDS, 1845: 174, plt. 43, fig. 44; CATLOW & REEVE, 1845: 288; REEVE, 1860, sp. 40, plt. 10; VREDENBURG, 1921: 344, no. 18

Terebra radula HINDS, 1844: 155 [non GRAVENHORST, 1807] [not figured]; HINDS, 1845: 74, plt. 44, fig. 95; CATLOW & REEVE, 1845: 290; REEVE, 1860, sp. 68, plt. 15

Terebra petiveriana DESHAYES, 1857: 85, fig. 10; TRYON, 1885: 14, plt. 3, no. 31; TOMLIN, 1944: 14, no. 141

Terebra glauca HINDS, 1844: 155; REEVE, 1860: sp. 40, plt. 10; TRYON, 1885: 14, plt. 1, fig. 19 [exclude from synonymy of *T. variegata* Gray, 1834]; PAETEL, 1888: 251; TOMLIN, 1944: 14, no. 142

Description of Species: Size medium, to 46 mm; color usually gray to brown, with whitish subsutural band, occasionally monochromatic flesh to beige; outline of whorls convex, with moderately wide convex subsutural band; protoconch of 3 to 3½ slender, glassy whorls; early whorls of teleoconch sculptured with elongate nodes on subsutural band and straight, sharp axial ribs; suture well defined; spiral grooves appearing about 4th whorl, sometimes developing small nodes upon crossing axial ribs about 7th whorl; sculpture coarse and extremely variable, of axial ribs with narrow spiral grooves or noded with broad grooves; subsutural band thick, convex, noded, well marked by suture and deep subsutural groove; body whorl with rough sculpture often continuing to siphonal fasciole; outer lip moderately sturdy, columella recurved, with 2 basal folds; siphonal fasciole striate, with keel.

Type Locality: Panama.

Type Specimens: Holotype and 1 paratype, British Museum (Natural History).

Remarks: It is interesting to note that after Reeve figured a specimen of *Terebra petiveriana* as *T. glauca*, subsequent reviewers followed his lead and figured *T. petiveriana* as *T. glauca* or synonymized *T. glauca* with *T. aspera* or *T. radula*, both synonyms of *T. petiveriana*.

Terebra carolae Bratcher, spec. nov.

(Figures 5, 7, 9, 11)

Synopsis: Shell medium-large with beige background marked with brown, flat sided except for convex subsutural band.

Description: Shell moderately large, 52.3 × 11.7 mm; color dull brownish-beige with darker brown between nodes of subsutural band and with light band at periphery of body whorl; outline of whorls flat, with convex subsutural band; protoconch missing from holotype and all mature specimens examined, but protoconch of immature paratype has 1½ smooth mamillate embryonic whorls; axial sculpture of early whorls of teleoconch of narrow ribs; spiral sculpture of subsutural groove cutting through ribs to form noded subsutural band, with 2 additional spiral grooves crossing ribs; axial sculpture of later whorls of weak ribs, 14 on penultimate whorl; spiral sculpture consisting of subsutural groove cutting through axial ribs and 4 rows of cords crossing over ribs to form indistinct nodes; spiral cords becoming obsolete on body whorl with 3 spiral grooves anterior to periphery, with numerous axial striae between periphery and siphonal fasciole; sutures deep; aperture long semi-quadrate; columella recurved, with weak plication; siphonal fasciole striate, keel very sharp, strong.

Type Locality: Santa Maria Bay, off Hughes Point, Baja California del Sur, Mexico (24°45'05"N; 112°19'W); 54 m, shell bottom.

Type Specimens: Holotype: LACM-AHF 11178. Paratypes, all from west coast of Baja California, Mexico: LACM-AHF 11184 from type lot (13); LACM 71-163 off Rompiente Point, 38 - 25 m (8); LACM A375 San Bartolomé Bay (21); LACM-AHF 71-164 off Rompiente Point, 50 m (9); LACM 71-178 San Pablo Point, 23 - 30 m (1); LACM 71-180 Point Pequena, San Juanico Bay, 10 m, fine sand (8); AMNH 18661 San Bartolomé Bay, 18 m (1); ANSP 345789 Cedros Island, 15 m (1); Bratcher collection Santa Maria Bay, 15 m (6); San Ignacio Lagoon (14); San Bartolomé Bay, 36 - 54 m (7); CAS 59672 Santa Maria Bay, 15 m (1); Cernohorsky collection Santa Maria Bay, 15 m (2); DuShane collection

USNM 782511 Santa Maria Bay, 15 m dredged.

Cedros Island (2); MCZ 28805 San Bartolomé Bay (1); YPM 17717 Santa Maria Bay (1); Skoglund collection off Cedros Island (20); SBMNH 51671 Santa Maria Bay (1); SDMNH 70581 Santa Maria Bay (1); BM(NH) Santa Maria Bay (1).

Discussion: This species most closely resembles *Terebra variegata* Gray, 1834, but it bears some resemblance also to *T. armillata* Hinds, 1844, both of which have slender, multistriate protoconchs. *Terebra carolae* has a paucispiral mamillate protoconch and a consistently wider apical angle than either of the 2 species mentioned above. The plications on the exterior columella are less pronounced, and the interior columella shows an even greater difference. That of *T. variegata* has 2 closely spaced, extremely sharp plications, while *T. carolae* has 2 wider spaced and weaker plications. *Terebra carolae* should be compared with *T. tiarella* Deshayes, 1859, which is smaller and monochromatic.

This species is named in honor of Carol Skoglund, who first brought it to my attention.

ABBREVIATIONS

Abbreviations have been used for a number of institutional collections cited in this paper. They are:

AHF – Allan Hancock Foundation (material on loan to Los Angeles County Museum of Natural History)
AMNH – American Museum of Natural History
ANSP – Academy of Natural Sciences of Philadelphia
BM(NH) – British Museum (Natural History)
CAS – California Academy of Sciences
LACM – Los Angeles County Museum of Natural History
MCZ – Museum of Comparative Zoology, Harvard University
SBMNH – Santa Barbara Museum of Natural History
SDMNH – San Diego Museum of Natural History
USNM – United States National Museum
YPM – Yale University Peabody Museum of Natural History

ACKNOWLEDGMENTS

I wish to express my thanks to Dr. A. Myra Keen for reading and evaluating the manuscript of this paper.

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A New Indo-Pacific Terebrid

BY

TWILA BRATCHER

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(1 Text figure)

IN 1969 AN UNUSUAL terebrid was dredged from 300 m in Hawaii by E. R. Cross. Though subsequent research showed it to be a new species, there was a hesitancy in describing it on the basis of a single specimen, particularly as the protoconch was missing. Since that time other specimens of the same species have been sent to me for identification from several areas of the tropical Indo-Pacific.

Because E. R. Cross was the instructor of my first course in underwater safety and is a longtime friend, because of his years as editor of the Hawaiian Shell News, and because he discovered the first specimen of this new species, I now take pleasure in naming it in his honor.

band about 5th whorl; sculpture of later whorls cancellate, with spiral and axial cords of about equal strength, forming small nodes at intersections, axial cords beginning at nodes of anterior band; double band occupying about half of whorl; cancellate sculpture continuing on body whorl to row of slightly enlarged nodes at periphery; spiral cords continuing anterior to periphery, axial sculpture becoming obsolete; aperture quadrate; columella recurved, with moderate parietal callus and scarcely visible plication; siphonal fasciole striate, with moderate keel.

Dimensions: Holotype 42.0 × 7.2 mm. Paratypes from 21.4 × 5.4 mm to 82.9 × 13.1 mm

TEREBRIDAE Mörch, 1885

Terebra Bruguière, 1789

Terebra Bruguière, Encycl. Méth. Hist. Nat. Vers 1: xv. Type species by SD (LAMARCK, 1799) *Buccinum subulatum* Linnaeus, 1767. Recent; Indo-Pacific

Terebra elliscrossi Bratcher, spec. nov.

Diagnosis: A medium to large sized white *Terebra* with small fulvous dots, cancellate sculpture, and a double subsutural band.

Description of Holotype: Shell size medium, color white with small round fulvous dots, usually in pairs, scattered at random; outline of whorls slightly concave with double convex subsutural band, anterior one being smaller; protoconch missing, but protoconch of paratype having 3½ slightly convex embryonic whorls; sculpture of early whorls of teleoconch consisting of narrow subsutural band with small nodes, followed by slightly curved axial ribs; spiral sculpture developing about 3rd whorl; posterior end of ribs swelling into nodes, forming second subsutural



Figure 1

Holotype of *Terebra elliscrossi* Bratcher, spec. nov.

Type Locality: Honolulu side of Pearl Harbor entrance, Honolulu, Hawaii, 21°17'N; 157°56'W at 300 m, sand and coral rubble bottom; *leg.* E. R. Cross, 10 May 1960

Type Material: Holotype Los Angeles County Museum of Natural History no. 1257. Paratypes: Australian Museum no. C111658 (1); British Museum (Natural History) (1); Bratcher collection (2); E. R. Cross collection (1); Western Australian Museum (1); R. Schoening collection (1) [all above paratypes from 21 to 37.5 m, Guadalcanal, Solomon Islands.] B. Parkinson collection (1), New Guinea; R. Schelling collection (1), Okinawa at 45 m; U. S. National Museum no. 71899 (1), 104 km SW of Cap St. André, Madagascar, 150 - 300 m.

Discussion: Some individuals of this species have finer sculpture, and the intersections of axial and spiral sculpture may be less likely to form nodes at the intersections. The larger specimens tend to become less coarsely sculptured in later whorls. Some specimens have many tiny fulvous dots; others have few, scarcely noticeable ones.

Terebra elliscrossi should be compared with several other Indo-Pacific species. *Terebra waikikiensis* Pilsbry, 1920, an endemic Hawaiian species, is also shiny white with pairs of small fulvous dots, but it has a turreted outline and is smaller, to 35 mm. The dots, always in pairs, are placed at regular intervals. *Terebra elliscrossi* has a concave outline with convex subsutural band, is larger, to 82.9 mm, and the dots, paired or individual, are scattered at random. *Terebra insalli* Bratcher & Burch, 1967, bears some resemblance to *T. elliscrossi* but has a smaller, more slender beige shell without the fulvous dots. *Terebra triseriata* Gray, 1834, has a much more slender shell, and that of *T. cumingii* Deshayes, 1834, has more numerous and shorter whorls, neither showing fulvous dots. *Terebra amanda*, also without dots, is longer whorled and has a wider apical angle.

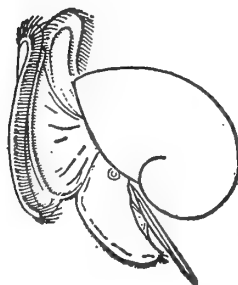
Terebra floridana Dall, 1889, a western Atlantic species, has a shell remarkably similar to that of *T. elliscrossi*, except that it has more numerous and shorter whorls with no dots, and is beige instead of white.

ACKNOWLEDGMENTS

I wish to express my gratitude to Brian Bailey of Guadalcanal, Solomon Islands, who collected most of the paratypes. I also want to thank E. R. Cross, Brian Parkinson, Ed Schelling, and Bob Schoening for the loan of type material for study, and Dr. A. Myra Keen for reading and evaluating this manuscript, and Bert Draper for taking the holotype photo.

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Lolliguncula panamensis

(Cephalopoda : Loliginidae)

from the Pacific Coast of Colombia

BY

H. J. SQUIRES¹ AND J. H. BARRAGÁN²

UNDP/FAO Proyecto para el Desarrollo de la Pesca Maritima en Colombia, Bogotá

(5 Text figures)

INTRODUCTION

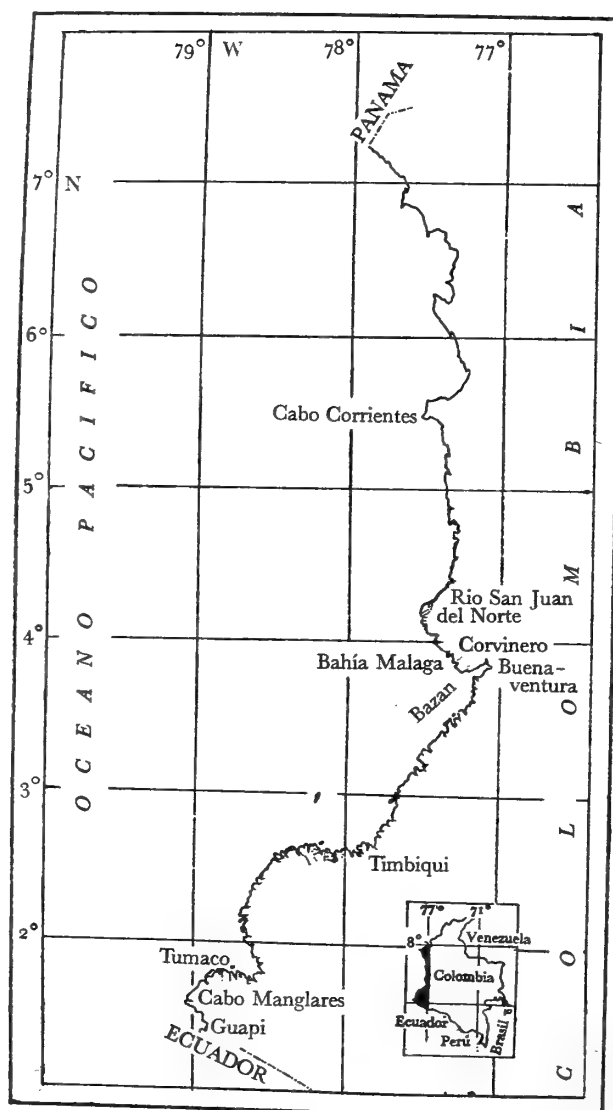
Lolliguncula panamensis Berry, 1911 is strictly a representative of the Panamic zoogeographical Province (OLSON, 1961) and is found only from Baja California to northern Perú. *Loliolopsis diomedae* appears to be similar in this respect although it is reported from deeper water than the former (VOSS, 1971). They are both taken in approximately the same depths where shrimp fishing is carried on off the coast of Colombia and Ecuador.

Squids of the genus *Lolliguncula* are shallow-living warm water species (DRAGOVICH & KELLY, 1967). Water temperatures for *L. panamensis* on the Colombian Pacific coast were 21° - 27° C at depths of 5 - 70 m (SQUIRES *et al.*, 1970; 1971), while for *L. brevis* on the Caribbean coast of Colombia they were 26° - 29° C at 10 - 35 m (LOPEZ, 1972). Where *L. panamensis* is taken the coastal area has fringing mangroves and many long estuaries with discharges of muddy water from rivers of the tropical rain forest. Secchi disc readings were 0.2 - 4.5 m in 5 - 10 m deep, and 3 - 12 m in 10 - 70 m deep, and salinities about 15 - 23 ppm (SQUIRES *et al.*, 1975).

(adjacent column →)

Figure 1

Distribution of squid, *Lolliguncula panamensis*, along the Pacific coast of Colombia, and names used in the text



Present addresses:

¹ 122 University Avenue, St. John's, Newfoundland, Canada² Instituto Nacional de Pesca, Casillo de Correos 5918, Guayaquil, Ecuador

Both *Lolliguncula panamensis* and *L. diomedae* were caught incidentally in shrimp trawls during survey fishing for shrimps (SQUIRES *et al.*, 1970; 1971). However, only small numbers of *L. diomedae* were taken and are not included in this study. Commercially, only the largest of the squids, mainly *L. panamensis*, are selected during shrimp fishing, and packed and frozen at the processing companies for export to Europe. Total catch reported at Buenaventura in 1970 was 37 tons.

During the survey for commercial shrimps and fishes, a chartered 22.5 m shrimp trawler used paired trawls, each with an effective opening of about 20 m wide and 2 m high. Stretched meshes were 40 - 43 mm in the wings and 34 - 41 mm in the codend of the trawls when wet. Towing speeds were about 3 knots. A series of 5 trawling stations in depths of 10, 20, 35, 55 and 70 m, respectively, were done at each of 16 shrimping areas along the coast. Stations north (or south) of Buenaventura were done in alternate months (SQUIRES *et al.*, 1970; 1971) during 1969 and part of 1970.

In the process of separating shrimps, fishes and various invertebrates in the catches, the few squids were counted, weighed on a commercial balance and preserved in 10% formalin in sea water.

After about 18 months in preservative, the squids were examined over a period of about 4 months in the laboratory at Buenaventura. Each sample was first soaked for about $\frac{1}{2}$ hour in fresh water, and lengths of mantle and tail fins measured on a measuring board marked in mm, or with vernier calipers. Total weight of each was taken on a precision balance (accuracy 0.1 g) after draining off excess liquid. Mantles were cut open and head and viscera removed. Mantles, gonads and nidamental glands were weighed separately on the balance. Ovaries were examined and ova diameters measured on a mm grid under 10 \times magnification.

Stomachs were opened in a watch glass and contents examined under magnification of 10 - 30 \times .

IDENTIFICATION

The 2 species were separated by the following main characters in mature squids:

- A₁ Body short and thick; tail fins forming an ellipse in outline and reaching about $\frac{1}{2}$ the length of the mantle. Only the left ventral arm hectocotylized in adult males. Suckers of arms with 5 teeth and of tentacular clubs 21 - 25 teeth *Lolliguncula panamensis*

- A₂ Body slender; tail fins forming roughly a semicircle in outline and reaching about $\frac{1}{3}$ the length of the mantle. Both ventral arms hectocotylized in adult males. Suckers of arms with 10 - 11 blunt teeth and of tentacular clubs 24 squared teeth *Loliolopsis diomedae*

BIOLOGY

Length-weight Relationships: Females of *Lolliguncula panamensis* were substantially larger than males (Figure 2) and greater in total weight for their length (Table 1). Average mantle weights were also slightly greater in females than in males at given mantle lengths. Regression equations where L = mantle length were:

Mantle Weight = $0.00794 L^{2.6937}$ in males (N = 93); and

Mantle Weight = $0.008667 L^{2.7205}$ in females (N = 547). Also

Total Weight = $0.00288 L^{3.305}$ in males (N = 92); and

Total Weight = $0.004284 L^{3.719}$ in females (N = 550) (BARRAGÁN, 1972).

Mantle weights were slightly more than 55% of the total weight in males (55 - 57%) and about 50% of the total weight in females (59 - 50%; Table 1). This difference can be explained by the large ovaries and nidamental glands in females contributing more to the total weight than testes and spermatophore glands in males.

Fin length (FL) increased slightly in proportion to mantle length (ML) with increase in size. Regression equations were as follows:

FL = $0.521 ML - 0.94$ in males (N = 94); and

FL = $0.555 ML - 1.14$ in females (N = 552) (Figure 3) (BARRAGÁN, 1972)

Growth Estimates: Growth increments in females were estimated from apparent shifts in modes of mantle lengths in frequencies within months and between months from samples taken during January-October, 1969 (Table 2; Figure 4). Average increment estimated within months is 19 mm and between months, 16 mm. Three modal classes were apparent in most months with differences of 10 - 36 mm (Table 2). Identifying modal shifts between months was based on most of the possibilities between successive months or every second month. Very small or very large apparent shifts were not included (Figure 4; Table 2).

Data for males were too few to give definitive results.

Table 1

Average Total and Mantle weights of *Lolliguncula panamensis* and percent mantle weight of total weight at given mantle length (96 males; 549 females).

ML	Frequencies		Av. Total weights		Av. Mantle weights		Percent Mantle weight of Total weight	
	M	F	M	F	M	F	M	F
			g	g	g	g	%	%
34	1	2	3.1	3.4	1.7	1.7	55	50
38	3	3	4.2	4.6	2.3	2.3	55	50
42	15	6	5.4	6.0	3.0	3.0	56	50
46	23	30	7.1	7.8	3.7	3.9	52	50
50	19	33	8.3	9.7	4.7	4.8	57	49
54	17	53	10.3	12.0	5.8	6.0	56	50
58	8	41	12.5	14.6	7.1	7.2	57	50
62	5	32	15.1	17.5	8.5	8.9	56	51
66	3	43	17.5	20.7	10.0	10.3	57	50
70	1	33	21.2	24.3	11.7	12.1	55	50
74	1	39	24.1	28.2	13.6	14.0	56	50
78		38		32.6		16.2		50
82		27		37.3		18.6		50
86		41		42.5		21.1		50
90		38		48.1		23.9		50
94		46		54.1		26.9		50
98		26		60.6		30.1		50
102		9		67.5		33.6		50
106		8		75.0		35.3		50
110		1		82.9		41.3		50

Table 2

Estimates of increments in mantle length between modes in length frequencies (Fig. 4) of female *Lolliguncula panamensis* from January-October, 1969.

Month 1969	Modal classes mm	No. of females	Increments within groups mm	Increments between months mm	Intervals between months
Jan	44, 64, 78, 88	63	20, 14, 10	30, 20, 28	Jan-Feb, Jan-Mar
Feb	44, 80, 94	27	36, 14	20, 48, 28	Feb-Mar, Feb-Apr
Mar	52, 64, 92	138	12, 20	28, 12, 36	Mar-Apr, Mar-May
Apr	44, 68, 92	35	24, 24	20, 32, 12	Apr-May, Apr-Jun
May	48, 64, 88	59	16, 24	12, 24, 40	May-Jun, May-Jul
Jun	76	21	—	12	Jun-Jul
Jul	48, 72, 88	83	24, 16	12, 24, 36	Jul-Aug, Jul-Sep
Aug	84	47	—	—	—
Sep	52, 76, 92	55	20, 12	24, 16	Sep-Oct
Oct	52, 76, 92	24	24, 16	—	—
Total females		552	Av. 19 mm	Av. 16 mm	
			Overall average 17 mm		

Maturity of Females: Four phases of maturity are defined based on ova diameter, weights of ovaries and nidamental glands, and color of ova in preservative (Table 3). The phases are categorized as Immature or Juvenile, Maturing, Mature, and Spent-and-recovering. An aver-

age of 59% of all females in samples were immature. Size of first mature was 80 mm in mantle length.

According to proportions of Mature or Spent-and-recovering in monthly samples, spawning occurred throughout the 10 months during which samples were collected. Appearances of ovaries also indicate that females spawn more than once after maturing (Table 3). The proportion of mature females ready to spawn (Phase III) or

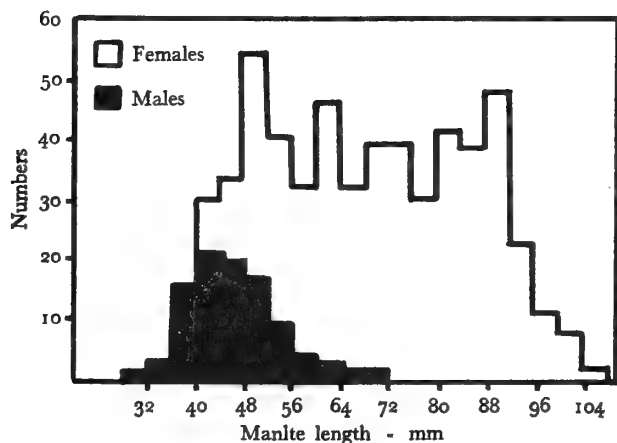


Figure 2

Length frequency histogram of 96 male and 552 female *Lolliguncula panamensis* taken from January to October, 1969, on the Pacific coast of Colombia

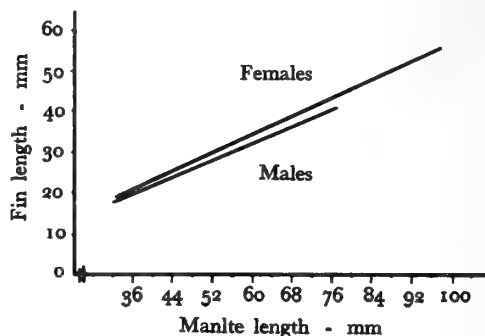


Figure 3

Regression of fin length (FL) on mantle length (M) of *Lolliguncula panamensis*. $FL = 0.521 ML - 0.94$ in 93 males; $FL = 0.555 ML - 1.14$ in 550 females

Table 3

Phases of maturity of female *Lolliguncula panamensis* from the Pacific coast of Colombia.

Phase	Category	Mantle length range mm	Weights of of nidamental glands g	Weights of ovaries g	Greater diameter of ova g	Color of ova	Presence of oocytes	Remarks
I	Immature or juvenile	32-75	0.1-0.5	0.3-1.5	0.1-0.3	Opaque white	Yes	Pyriform oocytes and small developing opaque ova attached to a dorsal (germinal) strand with branched stromae.
II	Maturing	74-79	0.7-1.8	1.8-3.2	0.5-1.0	Opaque yellowish	Yes	
III	Mature	80-110	1.8-4.0	3.0-8.5	1.0-1.8	Translucent yellowish	Yes	
IV	Spent and recovering	80-110	0.3-1.9	0.9-2.5	0.1-1.8	Opaque white but some yellowish	Yes	A few large residual ova translucent yellowish but degenerating.

recently spawned (Phase IV) averaged 73% in each month (range 63 - 87% with one exception of 41% in May; Table 4).

Maturity of Males: In the samples examined all males were maturing or mature (with spermatophores ready for transferral). All had the left ventral arm hectocotylized. The smallest was 34 mm in mantle length.

Stomach Contents: Most of the squid (81%) with food in their stomachs had remains of fishes: scales, spines, vertebrae, dark integument, muscle tissues, etc. These appeared to be fragments of small pelagic fishes common in the area, *i. e.*, engraulids (*Cetengraulis* spp.) and clupeids (*Opisthonema* spp.). Also present (in 15% of the stomachs) were remains of crustaceans, possibly small shrimps of the species *Xiphopenaeus riveti* and others.

As noted by DRAGOVICH & KELLY (1967) for small *Lolligunculus brevis* in Florida, BARRAGÁN (1972) men-

tions that most (70%) of the immature squid examined had empty stomachs, while only a few (24%) of the mature squid were empty. He also found that more (70%) of the early mature or maturing squid had food in stomachs than late matures (40 and 60%, respectively). Males and females of the same size were not significantly different.

DISCUSSION

Estimation of Stock Potential: Squids caught during survey fishing for shrimps and fishes on the Pacific coast of Colombia, were found throughout the area, but mostly in depths of 5 - 30 m (SQUIRES *et al.*, 1970; 1971). In a few parts of the area, such as off headlands, untrawlable grounds may form sanctuaries for squids and some species

Table 4

Percent of adult female *Lolliguncula panamensis* in maturity Phases III and IV (ready to spawn or recently spawned: Table 3) each month from January-October, 1969, on the Pacific Coast of Colombia.

Month	Total No. examined	Total No. of adults (Phases II, III & IV)	Percent in Phases III & IV
Jan	81	34	74%
Feb	26	13	87
Mar	141	61	85
Apr	36	18	88
May	63	16	41
June	26	15	87
July	87	22	63
Aug	48	30	83
Sept	59	17	74
Oct	24	11	73
Totals	591	237	
Average %			73

Table 5

Incidence of principal food items in stomachs of *Lolliguncula panamensis* (% of stomachs containing food item) from the Pacific coast of Colombia. Total examined, 468; empty, 280.

Principal food items	%
Small pelagic fishes such as engraulids and clupeids (fragments of scales, vertebrae, dark pigmented integument, muscle tissue, otoliths, etc.)	81
Crustaceans (fragments of mouth parts, limbs, integument)	15

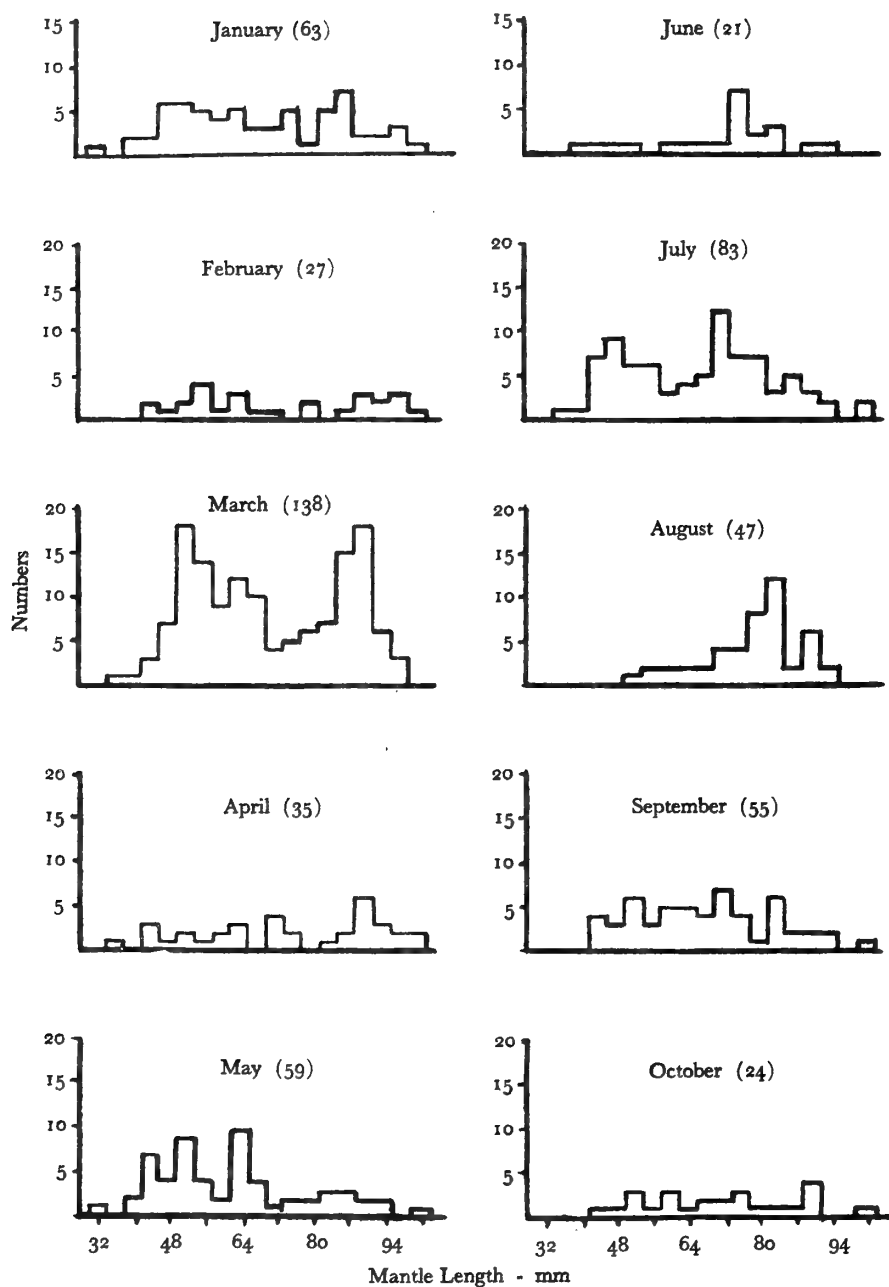


Figure 4

Monthly frequencies of mantle lengths of *Lolliguncula panamensis*
from the Pacific coast of Colombia, January to October, 1969

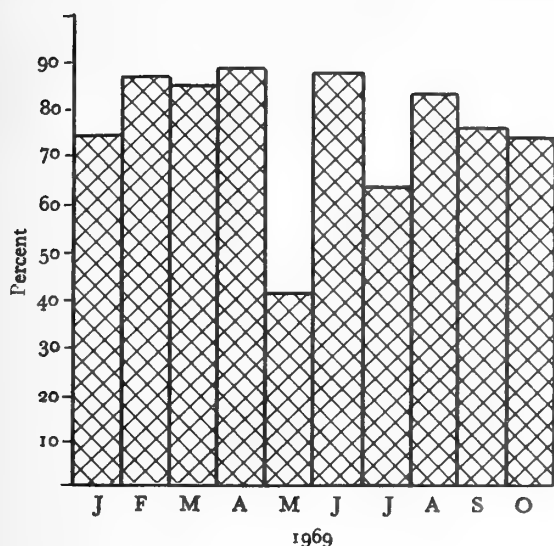


Figure 5

Percentages of ready-to-spawn and recently-spawned female *Lolliguncula panamensis* of mature females from January to October, 1969, on the Pacific coast of Colombia

of fishes. The total area where squids could be taken approximates 8 500 km².

Catches of squids by the chartered shrimp vessel averaged 0.5 kg per 1-hour haul, the sweep of the nets being about 0.115 km², and catch per km² therefore averaged 4.3 kg. If other shrimp vessels caught squids at a similar rate, it should be possible to calculate their total catch from the number of hours they fished in a year. In fact, the fleet of 87 shrimp vessels fished approximately 300 000 hours in 1970, and at a rate of 0.5 kg per hour the total catch would be 150 000 kg (150 metric tons; SQUIRES *et al.*, 1971).

Assuming that the vessels brought in catches of squid for the last 4 days of a 12 day trip (because of the tendency of squid to spoil on ice), it may be assumed that they landed only $\frac{1}{3}$ of their catch. The reported landings of squid at Buenaventura was 37 tons in 1970. A smaller part of the fleet ($\frac{1}{8}$) landed at Tumaco where it could be assumed another 5 tons were landed, giving a total landing of 42 tons.

On the other hand, calculating the catch of squid for the total area of 8 500 km² from catch per km² of 4.3 kg by the survey vessel would give an amount of 36 550 kg (37 tons). This estimate would assume that 100% of the

squid in the path of the trawl were caught. This would be undoubtedly incorrect, since some squids could escape the slow movement of the trawl or through its meshes, and some could be schooling in the water above the nets when preying on pelagic fishes. It is likely that catchability of the trawls is much less than 100% for many species, including squids and fishes.

Since an estimate of the total catch for the area by the commercial fleet is available (150 tons), it may be possible to estimate the catchability by the following method:

Estimated Annual Catch per Total Area	Estimated Catchability
tons	%
37	100
74	50
148 (150)	25

It may be assumed, therefore, that the catchability of this species by the shrimp trawls used by the fleet and the survey vessel was about 25%.

From the latter assumption it is further possible to estimate the biomass of squids in the area using GULLAND's (1970) equation as follows:

$$1.25 \times 0.5 \times 0.6 \times \text{squid biomass} = 150 \text{ tons}$$

Therefore, the squid biomass = 400 tons

The potential annual yield is here assumed to be 150 tons, the natural mortality 0.6 and the catchability 25%. An increase in the rate of fishing for squids could not be recommended on the basis of these estimations, although, if the squid could be frozen immediately when caught, the landings could be increased if the fishing rate remained the same.

Growth: Estimates of growth in squids from modal classes, averages, ranges, etc., of mantle length frequencies by various authors have been reviewed and compared by SUMMERS (1971). Estimates for *Loligo pealei* were 13 - 15 mm and for *Illex illecebrosus* 20 - 30 mm per month. Also growth of laboratory-reared squids has been documented by CHOE (1966) for *Sepioteuthis lessoniana* and by LAROE (1971) for *S. sepioidea*, giving average monthly increments of about 21 mm in mantle length. In smaller squids (Sepiolinae) estimates were as much as 5 mm per month (BOLETZKY *et al.*, 1971). In a larger squid, *Doryteuthis plei*, estimates of 15 - 25 mm per month for mantle length increments were obtained in laboratory-reared animals (LAROE, *op. cit.*).

In view of the estimates of monthly growth in mantle length for various squids, our estimate from modal clas-

ses of an average of 17 mm per month for female *Lolliguncula panamensis* appears reasonable between mantle lengths of 40 and 94 mm (Table 2; Figure 4).

Reproductive Potential: The presence of more than one size of ova in ovaries and an area of oocyte proliferation (germinal strand) suggest that more than 1 batch of eggs is produced by individual females. Also the appearance of the ovaries full of translucent large eggs or spent and recovering with predominantly small maturing ova suggests that the eggs are laid in batches. Synchronization in spawning such as reported by TINBERGEN & VERWEY (1945) and LAROE (1971) is indicated in this species by bimonthly peaks (Figure 4), although samples and differences are small.

An average of 73% ready-to-spawn or recently-spawned (Phases III and IV, Table 3) in each of 10 monthly samples would indicate spawning every $1\frac{1}{2}$ to 2 months (SQUIRES, 1973). The uniformly high temperatures throughout the year would most likely influence the rate of oogenesis as they affect the rate of embryogenesis (McMAHON & SUMMERS, 1971).

Stomach Contents as Evidence of Feeding Behavior:

Fish fragments occurred in most stomachs indicating that the main prey is small pelagic fishes. The latter are very abundant, although only lightly exploited by industry (about 1 000 tons annually are made into fishmeal or canned for food; Oscar Arroyo, personal communication). Species of *Opisthonema* and *Cetengraulis* are apparently the most abundant, but several species of anchovies, silver-sides, etc., are also common. Some pelagic fishes are regularly taken in shrimp trawls, especially in shallow water, but they school mostly near the surface and great numbers tend to escape the trawl. Similarly, their predators, such as the squids, would also escape bottom trawls to a large extent. Squid stomachs had little evidence of bottom feeding such as mud particles reported for *Lolliguncula brevis* by DRAGOVICH & KELLY (1966).

Size Differences in Males and Females: Differences in mantle lengths and weights between males and females even before maturity reflect early dimorphism in this species. The few large females at the end of the size range (Table 1; Figure 2) may be caused by increased mortality at these sizes since the decrease in numbers is abrupt. In males, on the other hand, the decrease is noticeably more attenuate (Figure 2), perhaps as a result of increasing ability to escape the trawls. However, it is apparent that they do not grow any larger than samples indicate. They appear to mature at a much smaller size than females.

ACKNOWLEDGMENTS

We appreciate the assistance of Dr. Gilbert Voss of the University of Miami School of Marine and Atmospheric Science in identifying *Loliolopsis diomedea*. We are also indebted to many of our colleagues in Colombia and the captains and crews of survey vessels for assisting in collections of squids at sea, and to INDERENA for laboratory facilities at Buenaventura.

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An Attachment Structure in an Epiparasitic Gastropod

BY

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(1 Text figure)

AN ECTOPARASITIC LIFE STYLE generally involves the development of specialized organs of attachment, as in the case of flatworms and arthropods where an array of simple to elaborate hooks, suckers, and spines has been well documented. However, among gastropod mollusks, not only is the ectoparasitic habit rare, but the development of specialized attachment structures has only been reported in one species of prosobranch mollusk (VERRILL, 1897). No attachment organ with the possible exception of the foot has ever been noted in any of the ectoparasitic gastropods.

The opisthobranch gastropod family Pyramidellidae consists of ectoparasites that feed on the body fluids of other mollusks and polychaete worms using a stylet on the end of a protrusible proboscis (FRETTER & GRAHAM, 1949). CLARK (1971) reports that the pyramidellan, *Odostomia columbiana* (Dall & Bartsch, 1909), responds to the surface texture of its host, the mesogastropod, *Trichotropis cancellata* (Hinds, 1848). Also, the heavily spiny periostracum is highly attractive to this parasite, and has positive adaptive value in that it prevents the parasite from being dislodged by strong currents. Yet the parasites are seen to move freely over all parts of the shell and also are able to move from one host to another.

While in residence at the Friday Harbor Laboratories during the spring of 1978, I had the opportunity to study host-parasite relationships between these 2 species of gastropods. The snails were collected in what is called the "potato patch" of East Sound, off Orcas Island, Washington, in approximately 30 m of water. Approximately 52 specimens of *Trichotropis cancellata* were dredged and 46% were found to be infected with *Odostomia columbiana*. The mean number of parasites per host equaled 1.62 ± 0.64 S. D. The snails were maintained in the laboratory in a 30 gallon [108 L] capacity plexiglass aquarium that was supplied with running sea water.

In the first attempts to remove some of these small pyramidellans from the surface of their host, one slipped from the grasp of the forceps. This was a most fortuitous accident, for the *Odostomia* did not fall to the bottom

of the sea water-filled bowl, but was caught on the edge of the dorsal lip of the host's shell, approximately 7 mm from where it originally rested. It appeared to be held in place by a thread that was still attached to its former position on the surface of the shell. Removing the *Trichotropis* from the water, the attachment thread of the parasite became apparent under the dissecting microscope; so it appears that the thread has an optical density similar to that of sea water, since it is relatively invisible while under water. The attachment thread seems to be quite elastic and resilient, for when the *Odostomia* was carefully nudged away from the edge of the shell of *Trichotropis* with the tip of the forceps, it snapped back to its original position on the surface of its host. Stretching tends to reduce the elasticity of the thread, and if it is stretched more than 15 mm, the thread will break and the parasite will lose contact with its host. To test whether the parasites could re-establish their attachment threads, the following experiment was undertaken. Twelve *Odostomia* were removed from the surfaces of a number of *Trichotropis*, thus severing the attachment threads, and then placed on the surfaces of new hosts. By the following day, 9 of the parasites had re-attached, forming new threads.

An aqueous saturated solution of neutral red selectively stains the attachment threads, making them readily visible. Staining a shell of *Trichotropis* from which 2 *Odostomia* had previously been removed demonstrated at least 6 attached fragments. Since more attached fragments were visible than the number of parasites removed, it appears that the parasites are able to sever their own threads and produce new ones as they move about their hosts in a fashion similar to mussels utilizing their byssal fibers.

The thread originates from the extreme posterior ventral surface of the foot (Figure 1). The margin of the posterior region is plicate, and there appears to be a median central pore from which the thread emerges. In addition, there is a ciliated median groove running up the antero-posterior axis of the foot terminating near the tip of the propodium. The function or role of this groove

was difficult to determine and cannot be answered here.

LA FOLLETTE (1977) has noted in dead and dried *Chrysallida cincta*, also a pyramidellid, on *Norrisia norrisii* that the snails remain attached to their hosts. They may have been held in place by dried attachment threads.

Normally, in gastropods, the foot is the major adhesive organ. What adaptive function might be served by possessing an additional attachment structure? This question is best answered by looking at the habitat of the host and the feeding behavior of the parasite. YONGE (1962) records that *Trichotropis cancellata* is restricted to hard bottomed subtidal substrates, consisting mostly of dead bivalve shells, that are repeatedly buffeted by strong tidal currents. A suspension feeder, it is relatively sedentary by habit in that it moves as high as possible on a vertical surface and stays there. When feeding, *Odostomia columbiana* stations itself near the very edge of the aperture of the host's shell in order to reach the soft mantle tissues with its long proboscis. This appears to be a precarious position, even on a relatively sedentary host with a spiny periostracum, given the force of the turbulent water and the vertical orientation of the host. The development and evolution of the attachment thread as an additional "life line" has positive adaptive values for *O. columbiana*.

Such attachment threads in gastropods may be more common than first realized. VERRILL (1897) first noted threads of adhesive mucus formed by the foot glands of many land slugs and certain marine gastropods as well. He reports that the sargassum snail, *Litiopa bombyx* (Rang, 1829), attaches itself to its floating algal home by a thread of adhesive mucus. This was later verified by WALLER (1975) in *L. melanostoma*, a synonym of *L. bombyx* (ABBOTT, 1974). Cadet Hand (personal communication) has observed the dove shell, *Mitrella carinata* (Carpenter, 1865), that inhabits the rocky intertidal zone of the Pacific coast of the United States attaching itself to the substrate by a thread of mucus secreted by the foot. In addition, I have observed on at least 7 different occasions while snorkeling in the Florida Keys the bubble shell, *Bulla striata* (Bruguière, 1792), hanging from a mucus thread after having dislodged them from a vertical facing wall. Dr. Hand feels that such forms of attachment may be size-related in that all the gastropods that demonstrate this phenomenon are quite small, generally less than 12 mm in length. VERRILL (*op. cit.*) has hypothesized an evolutionary relationship between mucus threads and the byssal threads of the bivalve mollusks. He suggests that the earliest form of attachment was temporary, perhaps being aided by mucus secretion from the surface of the foot. He notes that "such a mode of adhesion to objects is common among planarians, small nemerteans, annelids, and the young forms of many groups at the present time"; also, "from such a primitive adhesive

foot the transition to a larger foot with more specialized cells situated in a groove for the secretion of stronger byssus-like threads of mucus would have been easy."

Thanks are in order to Dr. A. O. D. Willows, Director of the Friday Harbor Laboratories, for the many facilities afforded me while in residence at the laboratories.

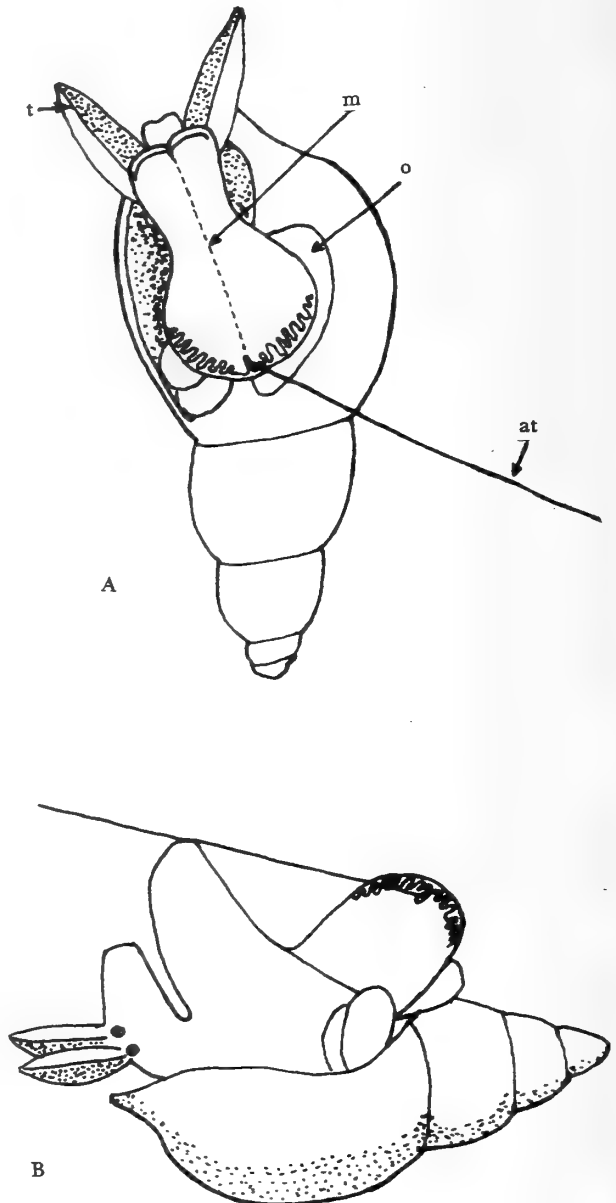
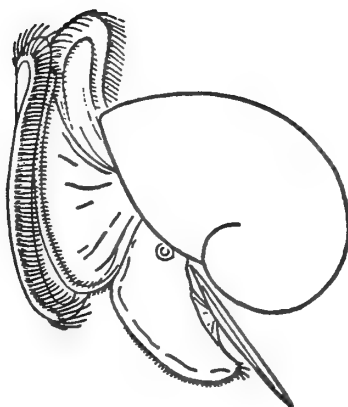


Figure 1

Ventral and lateral perspectives of overturned specimens of *Odostomia columbiana* showing relationships of attachment thread (at) to the foot. o - operculum t - ear-like tentacle
Snails are approximately 2 mm in length

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Predation upon *Crassostrea virginica* (Gmelin) Larvae by Two Invertebrate Species Common to Chesapeake Bay Oyster Bars¹

BY

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INTRODUCTION

THORSON (1950, 1966) DISCUSSED the high mortality of marine planktotrophic larvae and the dominant role played by predators in this mortality. MILEIKOVSKY (1974) expanded on this topic, concluding that the ecological significance of such predation was still unclear with more reliable quantitative data necessary. KORRINGA (1941) found that predation was the major cause of mortality in larvae of the European oyster (*Ostrea edulis* Linnaeus, 1758). Mature larvae of the American oyster, *Crassostrea virginica* (Gmelin, 1791), tend to be concentrated on or near the bottom of estuaries during ebb tide and slack water periods (CARRIKER, 1967; WOOD & HARGIS, 1971). Further, settlement of pediveliger larvae of oysters has been shown to be gregarious in nature (HIDU, 1969; HIDU *et al.*, 1970), presumably resulting in aggregations of larvae over suitable substrate in response to a water-borne pheromone (VEITCH & HIDU, 1971). Such gregarious behavior should increase mortality rate of larvae due to predation by benthic organisms, especially those invertebrates inhabiting shell surfaces of oyster bars which are major areas of oyster larval settlement (CRISP, 1967). In order to begin to establish significance of predation by such benthic invertebrates in Chesapeake Bay, in the summer of 1977 we investigated 2 common species, namely a sea anemone, *Diadumene leucolena* (Verrill, 1866) and a barnacle, *Balanus improvisus* Darwin, 1854.

Diadumene leucolena is found on oyster beds throughout Chesapeake Bay, occasionally occupying 15-25% of

the surface area of live oyster shells (CONES & HAVEN, 1969). Predation by sea anemones may be restricted mainly by their ability to seize and swallow prey, as annelids, mollusks and crustaceans can all be ingested (STEPHENSON, 1928). WILLIAMS (1972) found the main components of gut contents of *Diadumene luciae* (Verrill) to be amphipods, isopods and copepods. MACKENZIE (1977) recently reported preliminary observations that *D. leucolena* from Chesapeake Bay will feed on mature oyster larvae. We wished to quantify predation intensity, feeding rates and digestion times for this sea anemone.

SOUTHWARD (1955), BARNES (1959) and CRISP (1964) indicated that barnacles feed on a wide variety of planktonic organisms ranging in size from flagellates to small crustacea. Maturing oyster larvae may range in size up to 300 μ m (GALTSOFF, 1964; CHANLEY & ANDREWS, 1971), placing them within the reported size range of ingested material. *Balanus improvisus* is very common in Chesapeake Bay (WASS, 1972) often settling thickly on oyster shell. It should have every opportunity to prey on oyster larvae as they occur over oyster beds. We wished to test the assumption that *B. improvisus* will ingest mature oyster larvae.

We report here the results of our study of predation on mature *Crassostrea virginica* larvae by these 2 common invertebrate inhabitants of Chesapeake Bay oyster bars.

MATERIALS AND METHODS

Adults of both species were collected by oyster dredge in the Choptank River, Maryland (approximately 38°40'N; 76°10'W) during the summer of 1977. Pieces of shell carrying *Diadumene leucolena* or *Balanus improvisus* were chipped off oysters. Only sea anemones which remained

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attached to a shell fragment were used in experiments. This was generally true for *B. improvisus* as well, although occasionally barnacles not attached to a shell fragment but retaining their calcareous basis were used. All animals were maintained in aerated Choptank River water in the laboratory with collection and experimental salinities ranging from 9 to 11‰ over the summer. Experimental water temperatures were kept at 21° to 22°C, a few degrees Celsius below collection temperatures.

Oyster larvae were obtained from our laboratory's shellfish hatchery. Pediveliger or "eyed" larvae were collected on a 177 µm mesh screen and the younger umbo larvae on an 88 µm mesh screen. Water in which larvae were held was first filtered through a 10 µm filter. Over long holding periods, oyster larvae were fed cultured algae. During our experiments larval numbers were estimated as follows: Immediately after the water in their containers was mixed thoroughly with a non-rotary movement, a 1 mL sample was taken and the larvae therein were counted in a Sedgewick-Rafter cell. This was repeated 10 times and a mean value was determined and used to extrapolate to the number of larvae in the volume of water being sampled. When different prey densities were needed, they were obtained by concentrating larvae in a volume of water to a known larval density and then pipetting appropriate quantities of this "stock solution" (after brisk agitation) to filtered water to provide for the experimental densities desired.

Observations were made on individuals of each of the invertebrate species to observe their behavior in the presence of oyster larvae. In all experiments, individuals used were not fed in the 24 h period from time of collection until feeding observations began. Each invertebrate was placed in the experimental containers (11 to 20 cm diameter glass bowls) at least 6 to 18 h before larvae were introduced. Observations were made using a dissecting microscope at a magnification of 15 to 20×. Experiments were made on each of the species as follows:

Diadumene leucolena

Ingestion of Larvae: Observations were made over 15 to 60 min on feeding behavior of individual sea anemones in the presence of umbo and pediveliger oyster larvae and details were noted. During experimentation, 3 arbitrary size classes of *Diadumene leucolena* were used, based on pedal diameter of the attached animal: small (2 - 4 mm), medium (5 - 8 mm) and large (9 - 11 mm).

Two experiments were performed to study larval ingestion using varied densities of predator and prey. The

first experiment lasted 48 h and involved pediveliger densities of approximately 0.1, 0.4 and 1.6 larvae mL⁻¹ and the presence of either 2 medium sea anemones or 1 small, 1 large and 3 medium sea anemones. Controls contained no sea anemones. The second experiment lasted 24 h with larval densities of approximately 1.6, 3.2 and 6.4 larvae mL⁻¹ and predator densities of 1 or 2 medium sea anemones. At the end of each experiment, numbers of surviving larvae were determined by subsampling and in addition, the shell fragments and walls and floors of the containers were examined carefully for settled larvae (none were found).

Feeding Rates: Umbo or pediveliger larvae were added to 200 mL of water in 11 cm bowls containing single *Diadumene leucolena* which were then observed during feeding. Number of larvae ingested by sea anemones was counted over a 10 min period, beginning immediately after 1 larva was seen to be eaten. Ingestion was determined to occur when a larva travelled far enough down a sea anemone's pharynx to become lost from view. Size of sea anemone, larval density and larval stage were varied in these experiments.

Digestion Times: Sixteen individual sea anemones of varying sizes were allowed to ingest at least 10 pediveligers while under observation. They were then placed in water in clean bowls which were checked every 30 min for empty pediveliger shells. Time to appearance of shells was noted in each case.

Egestion and Gut Content Analysis: Forty-five sea anemones freshly dredged from the Choptank River were isolated on oyster-shell fragments, rinsed gently and then placed in individual clean glass bowls. Six to 12 h later, the shell fragments and bowls were examined for the presence of larval shells as evidence of predation on bivalve larvae in the field. In addition, gut contents of 1 laboratory-fed and 10 additional freshly dredged sea anemones were examined after dissection.

Balanus improvisus

Ingestion of Larvae: Two arbitrary size classes of barnacles were established based on greatest opercular diameter: small (2 - 4 mm) and large (5 - 8 mm). Known densities of umbo or pediveliger larvae were added to 11 cm bowls containing single barnacles which were beating their cirri. Control bowls contained no barnacles. After 18 h, the barnacles were removed, their shells and bowl surfaces were searched for settled oyster larvae and numbers of larvae surviving were determined by subsampling.

Egestion and Gut Content Analysis: Twenty-five freshly dredged barnacles were rinsed and placed in individual clean glass bowls which were examined 10 to 12 h later for shells of bivalve larvae. If feces were present, they were examined for larval shell fragments resulting from mastication by the barnacles (NICOL, 1967). If no feces were present, the barnacles' gut contents were examined after dissection. An additional 10 barnacles were allowed to sit and beat their cirri in a container containing pediveligers with a density of 20 larvae mL⁻¹ and their feces or gut contents, or both, were examined at intervals over a 10 to 12 h period.

Field Population Samples: We wished to determine densities of *Diadumene leucolena* and *Balanus improvisus* on oyster bars in Maryland's portion of Chesapeake Bay to estimate the potential for predation in nature. Sixteen oyster bars were sampled using a towed oyster dredge. Of the dredged material collected from each oyster bar, 30 L were shoveled into a container and the contents of the container (live oysters, shell, shell fragments) were then processed immediately by close examination of all surfaces of the dredged material. Total numbers of *D. leucolena* were readily obtained. Because of high densities of small barnacles, no attempts were made to differentiate between *B. improvisus* and *B. eburneus* Gould, 1841, another barnacle found in some parts of the Bay that we sampled; our data are counts of barnacles in general.

RESULTS

Diadumene leucolena

Feeding Behavior: Introduction of oyster larvae elicited pre-feeding behavior in *Diadumene leucolena* similar to that described by McFARLANE (1970) in *Tealia felina*. In *D. leucolena*, this behavior consisted of widening of the oral disc, raising and spreading of tentacles, and protrusion and opening of the actinopharynx. This pre-feeding response was quite stereotyped except for actinopharynx protrusion, which did not occur in some animals.

Feeding behavior in *Diadumene leucolena* was similar to that of *D. luciae* as described by WILLIAMS (1972), and his terminology is used here. The feeding response consists of 3 distinct actions: snatch, tentacular response, and oral response. The snatch occurs as a larva contacts and adheres to a tentacle which contracts quickly, although not completely. There is often a movement by the distal end of the tentacle to encircle the larva. A snatch response to a single larva never involved more than 2

tentacles. The tentacular response follows the snatch and consists of the tentacle bringing the larva to the oral disc, which begins to expand. The oral response occurs as the larva is transferred from the tentacle to the lips of the actinopharyngeal region, with the latter expanding outward toward the tentacle as the mouth opens. The larva is transported inside the anemone with the transport system almost certainly being the pharyngeal cilia, although these were too small to be seen.

An egestion response was observed in *Diadumene leucolena* that was similar to the oral response, with the direction of transport reversed. The mouth opened, although to a smaller extent than in feeding, and the egested larval shells were transported to the edge of the oral disc where they dropped to the substrate. Whenever more than 1 shell was egested at one time, the shells clung together in a clump.

Ingestion of Larvae: Table 1 contains results of the 2 ingestion experiments. Sea anemones fed heavily on pediveliger larvae as few larvae survived in the bowls with sea anemones whereas survival in control bowls was always much higher, usually by an order of magnitude. Decreased larval numbers in controls were presumably due to natural mortality and inevitable errors in sampling when adding larvae at the start of the experiments and counting survivors at the end. Variations in larval density and sea anemone size or numbers did not affect the results.

Feeding Rates: Results of feeding rate experiments are contained in Table 2. About 25% of the sea anemones initially used did not feed and were not considered when computing feeding rates. Rate variations were large, as would be expected for an individualistic process such as feeding. Rates were compared using Students' t-test after we had determined that variances were homogeneous as indicated by results of the Fmax-test (SOKAL & ROHLF, 1969). Feeding rate increased as larval density increased, with the differences statistically significant for medium individuals feeding on umbo larvae ($P < 0.05$; experiments 3 and 4) and pediveligers $P < 0.01$; experiments 7 and 8). Medium-sized individuals generally fed at a higher average rate than did smaller sea anemones, except in the presence of low densities of umbo larvae (experiments 1 and 3); however, these rate differences with size were statistically significant only for sea anemones feeding on high densities of pediveligers ($P < 0.05$; experiments 6 and 8). Small sea anemones ate fewer umbos min⁻¹ than pediveligers min⁻¹ whereas medium sea anemones ate fewer umbos min⁻¹ than pediveligers min⁻¹; these differences were not statistically significant ($P > 0.05$).

Table 1

Crassostrea virginica and *Diadumene leucolena*. Ingestion of pediveliger larvae under varying conditions of predator and prey density. Controls—no sea anemones. I. 48 h experiment. Water volume = 1.75 litres. Numbers of sea anemones per container: A—Two medium (5-8 mm pedal diameter); B—One small (2-4 mm), one large (9-11 mm) and three medium. II. 24 h experiment. Water volume = 0.25 litre. A—one medium sea anemone; B—Two medium sea anemones.

Approximate pediveliger density	Anemone density	Larval numbers			
		Replicate 1		Replicate 2	
		Start	Finish	Start	Finish
I. 0.1 ml ⁻¹	A	174	20	—	—
	B	174	3	—	—
	Control	174	118	—	—
0.4 ml ⁻¹	A	740	2	702	1
	B	740	4	702	1
	Control	740	697	702	102
1.6 ml ⁻¹	A	2775	6	2808	69
	B	2775	6	2808	20
	Control	2775	2147	2808	1006
II. 1.6 ml ⁻¹	A	400	13	400	3
	B	400	1	400	2
	Control	400	131	400	118
3.2 ml ⁻¹	A	799	16	799	0
	B	799	77	799	7
	Control	799	665	799	432
6.4 ml ⁻¹	A	1598	1	1598	38
	B	1598	2	1598	25
	Control	1598	826	1598	812

Table 2

Crassostrea virginica and *Diadumene leucolena*. Feeding rates of two sizes of sea anemone on two stages of oyster larvae. Single anemones in 200 ml of estuarine water were observed for 10 min after feeding began. N = number of replications. Feeding rate = average number of larvae eaten per minute \pm 1 standard deviation.

Experiment	Anemone Pedal diameter (mm)	N	Larval stage	Larval density (ml ⁻¹)	Feeding rate (min ⁻¹)
1	2-4	3	umbo	1	1.0 \pm 0.8
2	2-4	4	umbo	4	2.4 \pm 2.9
3	5-8	8	umbo	1	0.7 \pm 0.6
4	5-8	7	umbo	4	2.8 \pm 1.9
5	2-4	3	pediveliger	1	0.6 \pm 0.7
6	2-4	4	pediveliger	4	1.1 \pm 1.1
7	5-8	8	pediveliger	1	1.7 \pm 1.2
8	5-8	7	pediveliger	4	4.9 \pm 2.6

Digestion Times: Digestion time was considered to be the interval from the end of feeding to the first appearance in the experimental container of empty larval shell(s). A mean digestion time of about 4 h resulted. Results were generally consistent, with 8 out of 16 measurements falling in the 3.5 to 4.5 h range. The shortest interval of appearance of empty shells was 2.5 - 3.0 h; the longest was 5.0 - 5.5 h.

To check for digestion, the egested shells were examined. Of 163 pairs of hinged, intact shells examined, 133 (82%) were completely clear and empty. Of the remaining 30 pairs which retained some internal color or texture, none appeared to contain whole larvae.

Gut Content and Egestion Analysis: The gut of the 1 laboratory-fed sea anemone examined contained 50 pediveligers. Gut contents of 10 sea anemones freshly dredged from the Choptank River contained no bivalve larvae. Egested material from another 45 freshly dredged specimens collected at a later date yielded 1 complete pair of bivalve shells (comparable in size to those of oyster pediveligers) from each of 3 sea anemones.

Balanus improvisus

Ingestion Experiments: Results of these experiments are contained in Table 3. Compared with controls, larval

Table 3

Crassostrea virginica and *Balanus improvisus*. Effects of two sizes of barnacles on numbers of two stages of oyster larvae. Single barnacles left in presence of larvae in 200 ml of estuarine water for 18 h. Control bowls contained no barnacles. N = number of replications. Larval numbers at end of experiment are reported as mean \pm 1 standard deviation.

Experiment	Barnacle opercular diameter (mm)	Larval stage	N	Larval numbers	
				Start	Finish
1	2-4	umbo	8	404	74 \pm 58
2	5-8	umbo	8	404	51 \pm 60
3	Control	umbo	8	404	130 \pm 62
4	2-4	pediveliger	8	394	166 \pm 102
5	5-8	pediveliger	8	394	80 \pm 76
6	Control	pediveliger	8	394	273 \pm 39

Table 4

Diadumene leucolena and barnacles. Relative abundances on selected Chesapeake Bay oyster bars. Sample size per bar = 30 litres of oyster shell and associated material.

Oyster bar	Approximate location	<i>Diadumene leucolena</i>	Barnacles
Swan Point	38°08'N; 76°18'W	1	3583
Buoy Rock	39°00'; 76°13'	3	15943
Hood	38°56'; 76°14'	91	1289
Hollicutt Noose	38°51'; 76°21'	282	463
Cook Point	38°39'; 76°17'	377	78
Deep Neck	38°44'; 76°15'	250	782
Double Mills	38°44'; 76°08'	52	133
Horn Point	38°36'; 76°08'	75	378
Green Marsh	38°35'; 76°04'	48	458
Norman	38°15'; 76°07'	235	547
Middleground	38°14'; 75°55'	495	1049
Georges	38°08'; 75°50'	244	64
Marumsco	37°57'; 75°44'	287	749
Sandy Pt. North	39°01'; 76°23'	345	4282
Saunders	38°53'; 76°29'	36	1599
Cornfield Harbor	38°03'; 76°20'	153	873

numbers decreased markedly in bowls containing barnacles. Homogeneity of variances was established as before and t-tests indicated that large barnacles had a statistically significant effect on both umbo larvae ($P < 0.05$) and pediveliger larvae ($P < 0.001$) compared with control values. Small barnacles significantly affected only pediveliger numbers ($P < 0.05$). However, upon comparing effects of barnacle size on survival of umbo or pediveliger larvae (experiment 1 vs. 2; 4 vs. 5), no statistical differences were noted ($P > 0.05$).

Egestion and Gut Content Analysis: Examination of gut content and feces of 25 freshly dredged *Balanus improvisus* revealed no evidence of bivalve larvae ingestion, nor were any bivalve shells noted in the bowls. For the 10 barnacles active in the presence of pediveligers in the laboratory for up to 12 h, we noted the following: more than 30 semidigested larvae in the gut of a large barnacle examined 1 h after initial exposure; no evidence of larvae in the gut of a small barnacle examined 1 h after initial exposure; no evidence of larvae in the feces and gut contents of the 7 barnacles examined 10 to 12 h after initial exposure; and 2 dead pediveligers inside the shell plates of a large barnacle examined 30 min after initial exposure to larvae.

Field Population Samples: Table 4 contains the results of our survey of 16 oyster bars conducted on July 19 and 20, and August 8, 1977. Numbers of sea anemones present varied from 1 to 495 per 30 L sample of dredged material. In general, barnacles predominated, averaging 92% of the animals counted. On some oyster bars (e.g., Buoy Rock Bar), barnacles were extremely abundant, covering most of the available shell substrate. On other oyster bars (e.g., Cook Point, Georges) their numbers were relatively low.

DISCUSSION

Few reports exist regarding field densities of late-stage *Crassostrea virginica* larvae, and their gregarious nature in setting makes estimates ambiguous. HEDU & HASKIN (1971) reported a 200 L sample taken in Delaware Bay to contain 4786 "eyed" larvae (0.024 mL^{-1}). NELSON (1924) reported densities in his samples of up to 250 mature larvae L^{-1} (0.25 mL^{-1}). While these reported densities are comparable to the lowest larval densities used in our ingestion experiments with *Diadumene leucolella*, it was shown in our experiments that sea anemones would almost completely eliminate larvae over the range of 0.1 to 6.4 larvae mL^{-1} (Table 1). Larvae are used as food as evidenced by egestion of empty shells. We expect that, as oyster pediveligers aggregate (whether passively or actively) over oyster shell preparatory to setting,

sea anemones exact a toll, just as they did at the densities used in our experiments. *Balanus improvisus* (and presumably other species of barnacles in Chesapeake Bay) would appear to have a similar effect. Presence of semidigested larvae in one large barnacle exposed to pediveligers would indicate that the decline in larval numbers in the presence of barnacles (Table 3) is not just due to physical damage caused by contact with beating cirri but also involves feeding.

The few findings of oyster larvae in the guts of freshly dredged specimens of the invertebrate species cannot be construed as evidence that only limited ingestion of oyster larvae occurs in nature. We did not measure densities of oyster larvae in the water column over the oyster beds at the time of collection and our field collections were limited in number and over time. We expect that our laboratory observations demonstrating ingestion of oyster larvae by *Diadumene leucolella* and *Balanus improvisus* can be extrapolated to the field, although obviously these predators are exposed to a mixed food resource composed of more than just oyster larvae. There is no published evidence regarding selective feeding on oyster larvae in the presence of such a mixed resource. Nevertheless, when one considers the gauntlet of waving tentacles of sea anemones, beating cirri of barnacles, and filtering currents of adult oysters and an additional fouling species, the hooked mussel *Ischadium recurvum* (Rafinesque, 1820) (REICHARDT, 1977) it becomes obvious that loss due to predation may be very high near or at the time of settlement by oyster larvae.

SUMMARY

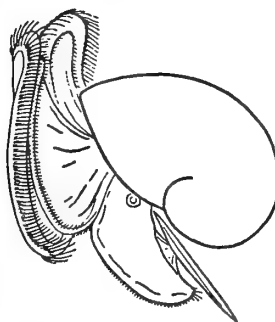
Predation upon umbo and pediveliger larvae of *Crassostrea virginica* (oyster) by *Diadumene leucolella* (sea anemone) and *Balanus improvisus* (barnacle) was studied in the laboratory. Pre-feeding and feeding behavior of *D. leucolella* in the presence of oyster larvae was described. Few larvae survived in the presence of sea anemones. As larval density increased, sea anemones' feeding rates increased, with larger individuals generally feeding at a greater rate than smaller individuals. At 21°C to 22°C , larval shells were expelled about 4 h after ingestion of living larvae by sea anemones had occurred, on average. In the presence of *B. improvisus*, numbers of surviving larvae decreased significantly. Pediveliger larvae were found in the gut of a barnacle which had been kept in their presence for 1 h. Examination of guts of very limited numbers of freshly dredged individuals from the field provided evidence of bivalve larval shell in *D. leucolella*, but not in *B. improvisus*.

ACKNOWLEDGMENTS

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NOTES & NEWS

Range Extension for

Penitella fitchi Turner, 1955

(Bivalvia : Pholadidae)

BY

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FOR THE PAST several years extensive dredging operations have been carried out in Monterey Bay in an attempt to determine the horizontal and bathymetric distribution of rock-boring bivalves. In addition, the intertidal sedimentary rocks of the northern part of Monterey Bay near Santa Cruz have been examined for borers and nestlers. Most of the bivalve borers found in this survey have been reported before from Monterey Bay, but one has not.

Penitella fitchi was described by TURNER (1955) from specimens collected by J. E. Fitch from sedimentary rocks exposed at the north side of Bahía San Bartolomé, Baja California, Mexico. At the type locality *P. fitchi* was fairly common along with about equal numbers of *P. penita* (Conrad, 1837) and a smaller number of *Chaceia ovoidea* (Gould, 1851). Subsequently a few other specimens have been found in southern California at Redondo Beach, La Jolla, and San Diego, and from near Isla San Geronimo, Bahía San Cristobal, and at Punta Pequeña, Baja California (KENNEDY, 1974). The specimen collected at La Jolla was a single dead shell found along with *Penitella gabbii* (Tryon, 1863), *P. penita*, *Netastoma rostrata* (Valenciennes, 1846), and *Lithophaga plumula* (Hanley, 1843) in a large intertidal zone mudstone cobble. KENNEDY (1974) also reported the rare occurrence of *P. fitchi* in the fossil record. Specimens have been found in late Pleistocene Palos Verdes Sand above Upper Newport Bay, California, and from Pleistocene deposits of San Pedro, California, and Bahía San Bartolomé, Baja California. In the California Pleistocene deposits *P. fitchi* was found associated with *Chaceia ovoidea*, *Netastoma rostrata*, *P. penita*, and *Barnea subtruncata* (Sowerby, 1834).

Of the several hundred pholads and boring mytilids collected in this survey by dredging sedimentary rock

from the shallow water of Monterey Bay, 2 living *Penitella fitchi* and 1 set of valves from a dead specimen have been found. The 2 living animals were recovered from hard siliceous chert of the Monterey Formation dredged in April and August, 1977, from water 25 m deep. The first animal was recovered from rock beneath the kelp bed off Del Monte Beach and the second from a reef outcrop east of Cannery Row, both sites near Monterey, California. In each case, *P. fitchi* was associated with numerous living *P. conradi* Valenciennes, 1846, *P. gabbii* and *Lithophaga plumula*. Each *P. fitchi* had a shell 50 mm long and 35.5 mm high and each was in the post-boring stage with a partial callum. The distinctive feature of this species of *Penitella* is the well-developed siphonoplax composed of numerous, flexible, over-lapping periostacal leaves. One of the specimens lived in an artificial burrow in an aquarium with running sea water for several months until preserved. The third specimen recovered during this study consisted of a pair of valves 40 mm long from a dead specimen in chert from water 15 m deep off Del Monte Beach. No specimens of *P. fitchi* have been found in sedimentary rocks from the intertidal zone in northern Monterey Bay.

The present known range of *Penitella fitchi* is therefore extended northward to include the southern part of Monterey Bay, California.

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Generous Donation

by the San Diego Shell Club

Shortly after our April issue was ready for mailing, we received from the San Diego Shell Club another generous donation to add to our Endowment Fund. We express our gratitude for the continued support by this organization. The income from the Endowment Fund materially assists and keeps on assisting in maintaining our very low membership dues and subscription rates.

A Correction

On pages 408 - 409 of volume 21 we have published a review by Mr. Barry Roth of the "Catalogue of Molluscan Taxa Described by Tadashige Habe During 1939 - 1975." Dr. Tôru Inaba has written to us regarding several errors: for KATURO OYAMA read KATSURA OYAMA (the co-author of this work), and for Okinaebisu-no-kai read Okinaebisu-no-kai; add after this: Masatoyo Okamoto. Further, the price is stated by Dr. Inaba to be \$30.00 (postage included).

UNITAS MALACOLOGICA

SEVENTH INTERNATIONAL MALACOLOGICAL CONGRESS
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The Congress will be held at Perpignan and Banyuls-sur-Mer in southern France. All topics about living or fossil mollusks are welcomed. The presentations may be made in English, French, or German. Abstracts will be published in "Malacologia." For detailed information write to: Secrétariat du 7ème Congrès International de Malacologie, Laboratoire de B. I. M et Malacologie, 55 Rue de Buffon, F-75005, Paris, France. Provisional registration by potential participants is requested. Forms for this purpose may be obtained from the Congress Secretary at the above address. It is recommended to do this as early as possible.

The Unitas Malacologica was formerly the Unitas Malacologica Europaea, but the name was changed to indicate that there is no discrimination against the participation of non-European malacologists; also, active membership is now open to all malacologists.

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A Glossary of A Thousand-and-One Terms Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US\$ 3.50 postpaid if remittance is sent with the order.

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We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US\$12.00 to US\$30.00, depending on the cost to us.

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At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

CALIFORNIA

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We are much disturbed by the steadily increasing number of premature claims for supposedly "missing" issues of our journal. Since we have announced on numerous occasions that our journal is mailed on the dates printed in the issues, *i.e.*, number 1 on July 1, number 2 on October 1, number 3 on January 1 and number 4 on April 1 of each volume year, it is unreasonable to expect delivery of the issues earlier than at least one week after these dates; however, a much longer time must be allowed for delivery to addresses at various distances from Berkeley. Thus, for example, a two weeks lapse is not unusual for as short distances as 500 km; and up to 3 and 4 months must be counted on for addresses in the Far East and in Africa. We are faced with the alternative of not replying to what we must consider premature claims or, if the trend continues, we must increase our subscription rates to cover these additional expenses. Our past efforts at keeping the subscription rate as low as possible are, we believe, sufficient evidence that we simply cannot afford any other course of action. The postal service causes us enough financial losses. Therefore we urgently request that before a claim is made, the time schedule be carefully checked. We are grateful for the understanding of this difficult situation shown by many librarians and will be grateful to those who, heretofore being perhaps eager to make sure that the library receives what is coming to it, will exercise a little patience.

Your harassed Editor.

BOOKS, PERIODICALS, PAMPHLETS

Biogeography and Adaptation: Patterns of Marine Life

by GEERAT J. VERMEIJ. xi+332 pp.; illust. Harvard University Press, Cambridge (Mass.) and London. \$25.00.
15 December 1978

This is a thoughtful, provocative, and at times speculative book, based primarily on studies of molluscan distribution and shell form, in which a mature zoologist draws together extensive observations on the adaptations of marine organisms to their physico-chemical and biotic environments. Patterns in form, behavior, and physiology are among the most intriguing that the marine world has to offer, and their geographic distribution is as legitimate a concern of the biogeographer as are patterns treated primarily in taxonomic-evolutionary terms.

In Part I (Patterns and Adaptations along Gradients), Professor Vermeij devotes Chapters 2 and 3 to gastropods and bivalves, respectively, and in Chapter 4 covers a variety of other slow-moving or sessile invertebrates, as well as plants. The author argues that physico-chemical conditions tend to provide the major selective forces in high and cold latitudes, but that biotic selective forces, especially predation pressure, result in greater defensive adaptations of prey species in more tropical waters. This is expressed in the evolution of such predation-resistant adaptations as armor, shell thickening, aperture narrowing, and shell sculpture in warmer seas. Further, Vermeij detects a comparable but micro-geographic trend in predator effectiveness and defensive adaptations of prey species in low as compared with high intertidal situations, and similarly in shallow as compared with deep environments.

The author's view that the biologically mediated component in the evolution of molluscan shell form is almost exclusively a response to predation, minimizing competition as a selective force, may be, however, the most potentially controversial aspect of the book. For example, narrow apertures that predominate in tropical gastropods are explained as a response to increased predation pressure. This view neglects the strong correlation of shell form with feeding mode and taxonomy in marine gastropods. Elongate apertures have evolved predominately in neogastropods (and in many mesogastropods that are also carnivorous) engaging in what is often a highly competitive business. In forms adopting an active, predatory mode of life, the elongation may be viewed as serving the dual functions of streamlining, particularly when elongation is coupled with detorsion, and of increasing the separation of inhalent and exhalent currents. This is not to argue for competition as the major selective force, but rather to point out that *both* competition and predation have exercised profound influences on molluscan form, physiology, and behavior.

In Part II (Interoceanic Patterns of Adaptation), Vermeij in Chapter 5 generalizes that the biotic pressures of grazing and predation among gastropods on open surfaces are greater in the tropical Indo-Pacific than in the tropi-

cal Atlantic, although this is not detectable in a number of other groups or on other substrates. Chapter 6 summarizes observations on the effects of present-day environmental factors such as water-movement, tides, salinity, temperature, and productivity on the establishment and maintenance of regional species diversity.

Part III (Geography and Evolution) becomes more general, as well as more varied in content than the title implies. In Chapter 7, Extinction and Speciation, Vermeij (without claiming originality) groups species into 3 categories rather than the 2 of the commonly-used "r-K-ic" system (the author may be forgiven a few other equally bad puns): (1) weedy or opportunistic species (r-selected); (2) stress-tolerant species adapted to variable or extreme environments; and (3) "biologically competent" species of stable and physiologically-favorable environments, the latter 2 groups comprising species commonly called K-selected. This and Chapter 8, Patterns of Biotic History, deal with both Recent and fossil communities, and are so varied as to be difficult to characterize succinctly. In the final Chapter 9, Barriers and Biotic Exchange, Vermeij examines biotic contacts between marine biotas as well as the problem of introduced species. The book ends with a discussion of the possible faunistic consequences of the opening of a sea-level, interoceanic, Central American canal. In this, as in all preceding chapters, Vermeij generalizes freely and frankly, often admitting the inadequacy of his data, but posing questions deserving further study. Perhaps the most important and valuable aspect of this book is that it represents a synthesis of a truly great amount of observation by a perceptive observer, who does not hesitate to express his carefully-qualified intuitions. This is not a book in which one can easily look up facts, although it is reasonably indexed, and indeed much of the discussion is difficult to follow if one is not broadly familiar with tropical molluscan and other genera.

Many of Vermeij's data consist of correlations and, as is always the case with such data, there are many possibilities for alternative interpretations and a lingering desire for substantiation. The tendency to speculation based on extensive observation has resulted in a book in which graduate students looking for research problems will find many a fascinating question. The text is very free of typographical errors, but Harvard University Press should be chided for the low quality of some of the half-tone figures. A 43-page list of references attests to the scholarly quality

of the book, and constitutes an invaluable resource. It is refreshing to find a book of this sort so free of "models" and so full of good observations and ideas.

Ralph I. Smith, Department of Zoology
Carole S. Hickman, Dept. of Paleontology
University of California, Berkeley

The Abalone Book

by PETER C. HOWORTH. Naturegraph Publishers, Inc.,
Happy Camp, California 96039. \$7.95 cloth; \$3.50
paper. 1978

Since Keith Cox's excellent "California Abalones, Family Haliotidae" (1962, Calif. Dept. Fish & Game, Fish Bull. 118) went out of print, I have been at a loss to recommend any available book as a ready source of information on eastern Pacific abalones, genus *Haliotis*. This popularly written manual will undoubtedly fill many buyers' needs. It contains a brief history of the abalone, from the fossil record to man's present-day impact, a section on problems plaguing the resource and some possible solutions, basic abalone biology, a review of North American species, and advice on preparation and cooking. There is a key to identifying west coast abalone shells and another for underwater identification. Shells of California abalones, interior and exterior, are illustrated on brilliant color plates. The colored figures of each species' epipodium are helpful for field identification by divers and sport fishermen. Northern California divers may take a second, hard look at the red abalone, *Haliotis rufescens*, in color plate I, for this appears to be a southern California form of the species, with reduced radial sculpture and elevated tremata — probably the result of introgressive hybridization with *Haliotis sorensi*. Hybrids between the two are particularly common in the Santa Barbara Channel area. The specimen illustrated as the Florida abalone, *Haliotis pourtalesii* (p. 65), differs in profile and sculpture from the original illustrations of that species.

"The Abalone Book" is rich in firsthand observations, based on the author's 24 years as a diver and 2 years managing an abalone processing plant. One can judge the depth of Howorth's involvement with abalones from his comment regarding *Haliotis cracherodii*: "Blacks are the Bogarts of the abalone world."

Barry Roth

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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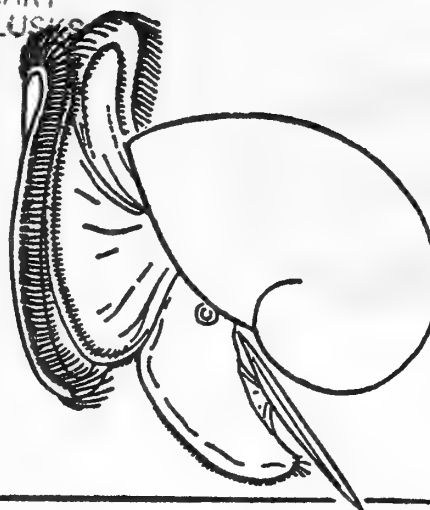
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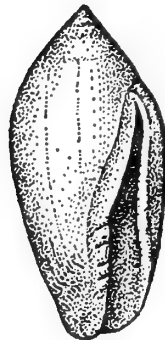
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University of California, Berkeley, CA 94720**

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
 SUPERFAMILY, FAMILY, Subfamily, Genus, (*Subgenus*)
New Taxa

The Family Epitoniidae

(Mollusca : Gastropoda)

in the Northeastern Pacific

BY

HELEN DUSHANE

15012 El Soneto Drive, Whittier, California 90605

(6 Plates; 3 Text figures)

INTRODUCTION

THIS PAPER IS A REVIEW of the late Neogene and Quaternary species of Epitoniidae (Mollusca: Gastropoda) which occur in the littoral and sublittoral zones of the northeastern Pacific, from Point Barrow, Alaska (171° 20' N) (including the Aleutian Islands) south to Cedros Island, Baja California Norte, Mexico (28° 12' N). Species occurring south of Cedros Island were treated previously by DUSHANE (1974).

This treatment is an attempt to characterize epitoniid species, discuss populational variation, summarize data on the ecology of the group, record the fossil occurrences, and to revise the nomenclature. The nomenclatural revisions herein have resulted in synonymizing some nominal taxa which hopefully will provide a better understanding of identity of other taxa.

Species of Epitoniidae display a confusing degree of morphological variability. Some early authors separated specimens on very trivial characters without realizing how widely dispersed epitoniids are. That populational variability exists has been established by DALL (1917), STRONG (1930, 1945), and others. The epitoniids of the northeastern Pacific region show considerable variation. In working with this family it soon became obvious that previous synonymies were incorrect, figures were inadequate, and very little was known of the infraspecific variation and distributional limits of most species. The synonymies here are intended to be complete, except for those treated previously by DUSHANE (1974). Figures of some earlier type material do not exist, and some types have subsequently been lost. Many published geographic ranges cannot now be substantiated with referred material. The ranges given are based on material examined for this study.

Useful references for the species in this family are: SOWERBY (1844); CARPENTER (1857, 1864); NYST (1871);

DALL (1917, 1921); DEBOURY (1919); STRONG (1930, 1937); GRANT & GALE (1931); DURHAM (1937); CLENCH & TURNER (1950, 1951, 1952); PALMER (1958).

Morphology: Of the supraspecific taxa recognized by CLENCH & TURNER (1950, 1951, 1952) only the genera and subgenera *Acirsa*, *Amaea*, *Asperiscala*, *Boreoscala*, *Depressiscala*, *Nitidiscala*, *Opalia*, *Sthenorytis*, and (*Scalina*) are used herein. *Epitonium* s.s. (type species *Turbo scalaris* Linnaeus, 1767), is characterized by convex, unattached whorls and does not seem to have typical members in the eastern Pacific. Certain morphological differences from those of *Epitonium* s.s. suggest that *Nitidiscala* and *Asperiscala* should be given full generic rank, which has been done herein.

Epitoniid genera can be characterized in the following ways:

Asperiscala: Usually turreted with a consistent pattern of cording or fine threads on the whorls, sometimes obsolete on later whorls; costae usually recurved, sometimes with a shoulder spine. In the eastern Pacific 22 species of *Asperiscala* are recognized from the tropical Panamic region (DUSHANE, 1974), and 6 from the temperate northeastern Pacific.

Nitidiscala: Not always turreted; lacking spiral sculpture between whorls; costae bladelike, reflected, or overlapping as in *N. catalinae*, with a sharp shoulder spine or extension, not continuous from whorl to whorl; basal disk lacking. From the tropical eastern Pacific 16 *Nitidiscala* species are recognized (DUSHANE, 1974); and 7 occur in more temperate waters.

In *Opalia*, the nominal subgenera *Nodiscala* and *Dentiscala* of De Boury have characters that are ill-defined and difficult to apply. They are not used herein. All *Opalia* have a heavy calcareous outer coat (intritacalx), that, when worn, removes the fine pitting characteristic of them, leav-

ing the shell with a shiny appearance. The purpose of the punctae is not yet known. The remaining genera and subgenera have diagnostic characters that make them readily recognizable and have been covered by CLENCH & TURNER (1950, 1951, 1952). Brief summaries of each are given under the separate headings.

The length and diameter of a shell for a given number of whorls and costae are probably the best characters for identifying species of *Epitonium*. The limits of specific variation in the number of costae are greater in those species having more costae. ANKEL (1938b) suggested that the costae are a defense against boring naticids, a suggestion that parallels my own observations. Few epitoniids show damage from boring predators. Many type specimens, unfortunately are beach-worn specimens and are too abraded to be of scientific value. Characters that are useful for separating species, are: size of shell, length and diameter of shell, number of whorls, number of nuclear whorls in relation to the remainder, sculpture and shape of early whorls, number and placement of costae on the whorls, absence or presence of spiral sculpture, presence of punctae (as in *Opalia*), absence or presence of a basal disk or cord, depth of suture, presence or absence of an umbilicus, shape and placement of aperture, sculpture of operculum, and geographical and bathymetric origin.

The internal anatomy of the epitoniids was partially described by THIELE (1928). The head includes the tentacles and eyes, the foot provides the animal with a means of locomotion, and the coiled visceral mass contains the internal organs. The foot is extended in front, grooved behind, ostensibly to help grip the surface, and with a thin, horny operculum. The long proboscis, when protruded, displays two specialized stylets alongside the mouth, which is at the base of the proboscis. The stylets, surrounded by a sheath of muscle, have openings for the salivary glands. There are no oesophageal glands. The hypobranchial gland produces a purple secretion. Other than the fact that it is a protein-like substance, we do not yet know the chemical constituents of the purple dye. ANKEL (1938a), THORSON (1958), and ROBERTSON (1963) suggested that this gland introduces an anesthetizing agent into its prey. Additional tests (SALO, 1977) suggested that *Epitonium* toxin inhibits some part of the neuromuscular system of the anemone on which it feeds. The structure of the buccal mass suggests that epitoniids can swallow their prey whole (FRETTER & GRAHAM, 1962). PERRAN (1978), in experiments with *Boreoscala greenlandica* (Perry, 1811), found this species could swallow whole the small anemone *Gonactinia prolifera*.

Epitoniids have two sharp-edged jaws near the buccal mass. HOCHBERG (1971), DUSHANE (1974), C. R. SMITH

(1977), SALO (1977), and PERRAN (1978) have shown that epitoniid radular teeth are different from all other prosobranch radulae with the exception of *Bulla* and *Ianthina*, which they most resemble. The numerous, evenly spaced, lateral teeth are arranged in regular rows forming obtuse angles. There are no central hooks as in other families of gastropods. The animal has an abnormally long acrembolic proboscis, which led FRETTER & GRAHAM (1962) to theorize that perhaps epitoniids have a method of feeding on either annelid worms or nemerteans that would require anesthetization before being seized by the radula. Subsequent observations have not borne this out (HOCHBERG, 1971, C. R. SMITH, 1977, SALO, 1977, PERRAN, 1978). The radula consists of a ribbon of cuticle with rows of teeth that lie flat within the buccal mass. As the radula slips forward, the teeth become almost vertically erect and ready to rasp. As the radula returns, a reverse action takes place. This action constitutes the food gathering habit of the epitoniids. A detailed account of this process is given in FRETTER & GRAHAM (1962).

HOCHBERG (1971: 22) noted that in southern California, *Nitidiscala tinctoria* lives in specific association with the small aggregate anemone, *Anthopleura elegantissima*, throughout its post-larval life. "This so-called micropredator is active twice a day during periods of high water when the anemone beds are covered and the polyps expanded. In order to feed, the snail everts a long acrembolic proboscis and slips it over the tip of a tentacle. The tentacle is held in place by the jaws and radula in combination with a muscular buccal bulb. Two stylets at the end of the proboscis inject a salivary toxin or anesthetizing agent. The tip of the tentacle is cut or torn off and pulled into the digestive system upon retraction of the proboscis." Hochberg's observations are corroborated by his excellent photographs. C. R. SMITH (1977) conducted experiments on the chemical recognition of prey of the same species. As a result, she also demonstrated that this gastropod is a micropredator on the anemone, *Anthopleura elegantissima*, its preferred prey, but will also eat the tentacles of *A. xanthogrammica*. The epitoniid also ingested tissue from two other Actiniidae, *Tealia lofotensis* and *Epiactis prolifera*, but less commonly. SALO (1977) corroborated the findings of both HOCHBERG (1971) and C. R. SMITH (*op. cit.*). SALO (*op. cit.*) also tested the feeding behavior of *Nitidiscala indianorum* and found that *Tealia crassicornis* and *T. lofotensis* were most commonly accepted.

THORSON (1958) observed *Opalia funiculata* [= *O. crenimarginata*] sucking on the body-cylinder of *Anthopleura* at mid-tide level. My observations in the field have been that *O. funiculata* and *O. borealis* attach themselves at the base of the anemone and not in the cup where the nema-

tocysts are located. Also, the anemone is partially contracted at this time. All the observations were made in the intertidal zone and in daylight. PERRAN (1978) found that unlike *Nitidiscala tinctoria*, *Boreoscala greenlandica* fed on the column of the large anemone *Metridium senile*, and swallowed whole the small anemone *Gonactinia prolifera*. He also found that over short distances epitoniids are able to locate their prey by chemotaxis.

Epitoniids are consecutive hermaphrodites, laying their eggs in small clusters, each cluster affixed to the next by a mucus thread. Those species with a habitat in or near sandy substrates have sand-agglutinated egg capsules, each capsule containing thousands of unhatched veligers. (Coral associated species do not have sand-agglutinated egg capsules.) As the eggs hatch, the veligers develop a smooth protoconch that is followed by whorls with costae or other characteristic sculpture.

METHODS AND FORMAT

The following outline has been adopted for each species:

Synonymy: Original species name, author, date of publication, page number(s), and figure number(s), if any, followed by like information for each author using the identical name.

Original Description: Even if the description is not in English, it is given verbatim.

Additional Description: Supplementary descriptions are given for all species. Most descriptive terms are subjective; however size (length) is defined herein as "small," 0 to 5 mm; "medium," 5 to 10 mm; and "large," 10 mm and over. The number of costae and range for each species is recorded in whole numbers, as is the number of nuclear whorls and post nuclear whorls.

Type Material: The repository of the holotype and any paratypes is listed with the type numbers. The same information is provided for each synonym, if any.

Type Locality: This is given, when reported by the original author, together with the collector's name, if known. The type locality is also given for any synonyms.

Distribution, Ecology and Bathymetric Range: Extremes of geographic and bathymetric range are given.

Geologic Record: (Contributed by George L. Kennedy.) Occurrences cited in this section are essentially only those

of the Section of Invertebrate Paleontology of the Los Angeles County Museum of Natural History (LACMIP). Additional published records are not included herein because it was not possible to examine the actual specimens cited. Literature citations, however, are included in the synonymy of each species, but the reader should be aware that these are unconfirmed occurrences. The specimens cited herein were identified by the author and arranged stratigraphically by G. L. Kennedy. Localities are arranged from north to south within each time-stratigraphic interval (lower Pliocene to upper Pleistocene).

Although it is becoming increasingly apparent that there is a great variation of ages within coastal Pleistocene deposits, it has not been possible to integrate this new chronology into this paper because of the lack of precise ages for many of the localities. Thus some classical "Pliocene" formations in Oregon and "lower Pleistocene" ones in southern California (Los Angeles basin) which are actually middle Pleistocene in age, are still cited herein as lower Pleistocene (in a two-fold division) for the sake of consistency with existing literature.

Following any fossil occurrences are cited a number of representative recent stations, also based on collections of the Section of Malacology (LACM), as well as documentation of southern and northern-most occurrences.

Discussion: Related information which is not applicable elsewhere is placed here. No attempt has been made to list all the locality data for each Recent species, as some records cannot be documented and some taxa are known from numerous records that would be cumbersome to report. In cases where the species is rare, all locality data are used; otherwise only the north and south extremes of the known range, together with literature documentation are listed.

Type Photographs: Photographs are of type specimens. If the type is badly worn, a photograph of a live-taken specimen is included.

ABBREVIATIONS

The following abbreviations are for institutions whose material has been used in this study:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania
AMNH	American Museum of Natural History, New York City, New York
BM(NH)	British Museum (Natural History), London, England
CAS(GTC)	California Academy of Sciences, San Francisco, California (Geologic Type Collection)

LACM	Los Angeles County Museum of Natural History, Section of Malacology, Los Angeles, California
LACM-AHF	Allan Hancock Foundation Collection, University of Southern California, now at the Los Angeles County Museum of Natural History
LACMIP	Los Angeles County Museum of Natural History, Section of Invertebrate Paleontology, Los Angeles, California
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
PRI	Paleontological Research Institute, Ithaca, New York
RM	Redpath Museum, McGill University, Montreal, Quebec, Canada
NMC	National Museum of Canada, Ottawa, Ontario, Canada
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California
SDNHM	San Diego Natural History Museum, San Diego, California
SU	Stanford University Collection, Palo Alto, California, now at the California Academy of Sciences
UCMP	University of California, Museum of Paleontology, Berkeley, California
USNM	United States National Museum of Natural History, Washington, D.C.

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† deceased

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SYSTEMATIC TREATMENT

EPITONIACEA Lamarck, 1822 [?1812]

[Nom. correct. et nom. transl., BERRY, 1910, *ex* Scalariana Lam.]

EPITONIIDAE Lamarck, 1822 [?1812]

[Nom. correct. BRODERIP, 1839, as Scalaridae, and BERRY, 1910, *ex* Scalariana Lamarck]

Epitonium Röding, 1798

[*Scala* of authors; *Scalaria* Lamarck, 1801]

Shells usually colorless, somewhat turreted, sometimes umbilicate, axial sculpture of heavy or slender costae, sometimes recurved; whorls numerous, with varying degrees of convexity, coiled either loosely or tightly; spiral sculpture present or absent; aperture round or oval; operculum thin, horny, paucispiral.

Acirsa Mörch, 1857

[Type species: (M) *Scalaria borealis* Lyell, 1841]
Outer lip thin; axial and spiral sculpture of low ribs; basal keel indistinct.

Table 1

Chart showing geographical ranges and fossil records reported herein.

<i>Acirsa borealis</i> (Lyell, 1841)	Circumboreal	
<i>Acirsa cerralvoensis</i> (DuShane, 1970)	23°N - 28°N	Pliocene, San Diego County, California
<i>Amaea (Scalina) brunneopicta</i> (Dall, 1908)	10°N - 28°N	Pliocene, San Diego County, California
<i>Amaea (Scalina) effiae</i> (Willett, 1939)		Pleistocene, San Pedro, California
<i>Asperiscala bellastriata</i> (Carpenter, 1864)	32°N - 37°N	Pliocene, Los Angeles and Orange Counties, California
		Pleistocene, same as above
<i>Asperiscala cookeana</i> (Dall, 1917)	24°N - 32°N	[Upper] Pliocene, San Diego County, California
<i>Asperiscala hemphilli</i> (Dall, 1878)		Pliocene, San Diego County, California
		Pleistocene, same as above
<i>Asperiscala lowei</i> (Dall, 1906)	24°N - 34°N	
<i>Asperiscala minutica</i> (DeBoury, 1912)	1°S - 28°N	Pliocene, southern California, Cedros Is., B.Cfa. Norte
		Pleistocene, Galápagos Islands, Ecuador
<i>Asperiscala tinctoria</i> (Dall, 1919)	24°N - 8°N	Upper Pleistocene, Orange County, California, Punta Pequena,
	24°N - 138°N	B. Cfa. Sur, Mexico
<i>Boreoscala greenlandica</i> (Perry, 1811)	50°N - 71°N	Pleistocene, Alaska
	163°E - 172°W	Pleistocene, Aleutian Islands
<i>Depressiscala polita</i> (Sowerby, 1844)	1°N - 33°N	Pliocene, Galápagos Islands, Ecuador
<i>Nitidiscala caamanoi</i> (Dall and Bartsch, 1910)	48°N	Pleistocene, San Pedro, California
<i>Nitidiscala californica</i> (Dall, 1917)	28°N - 33°N	Pliocene, Los Angeles and San Diego Counties, California
		Pleistocene, Los Angeles County, California
<i>Nitidiscala catalinae</i> (Dall, 1908)	28°N - 54°N	Pleistocene, Los Angeles County, California
<i>Nitidiscala catalinensis</i> (Dall, 1917)	31°N - 50°N	Pliocene, southern California
<i>Nitidiscala hindsii</i> (Carpenter, 1856)	14°S - 54°N	Pliocene, Santa Barbara County = Pleistocene, Santa Barbara
		County, California and Turtle Bay, B. Cfa. Sur, Mexico
		Pleistocene, from Santa Barbara south to San Diego Counties,
		California
<i>Nitidiscala indianorum</i> (Carpenter, 1865)	31°N - 54°N	Pliocene, Orange, San Diego Counties, California
		Pleistocene, Oregon and California
<i>Nitidiscala sawinae</i> (Dall, 1903)	24°N - 54°N	Pliocene, Los Angeles and San Diego Counties, California
		Pleistocene, Oregon and California
<i>Nitidiscala tinctoria</i> (Carpenter, 1865)	24°N - 54°N	Pliocene, Los Angeles south to San Diego Counties, California
		Pleistocene, Humboldt south to San Diego Counties, California
<i>Sthenorytis stearnsii</i> (Dall, 1892)	28°N	Pliocene, Pacific Beach, San Diego County, California
<i>Opalia borealis</i> Keep, 1881	31°N - 54°N	Pliocene, Los Angeles and San Diego Counties, California
		Pleistocene, Los Angeles County, California
<i>Opalia funiculata</i> (Carpenter, 1857)	3°S - 34°N	Pleistocene, Santa Barbara and Los Angeles Counties, California
<i>Opalia infrequens</i> (C. B. Adams, 1852)	8°N - 34°N	Pleistocene, Santa Barbara County, California
<i>Opalia montereyensis</i> (Dall, 1907)	25°N - 54°N	Pliocene, Los Angeles and San Diego Counties, California
		Pleistocene, Santa Barbara, Los Angeles, San Diego Counties,
		California
<i>Opalia spongiosa</i> Carpenter, 1866	1°S - 36°N	Pliocene, San Diego County, California
		Pleistocene, Los Angeles County, California
<i>Opalia varicostata</i> Stearns, 1875		Pliocene, Washington, California (San Diego, Orange Counties)
		and Baja California Norte, Mexico

Acirsa borealis (Lyell, 1841)

(Figure 1)

Scaloria borealis LYELL, 1841: based on Philos. Trans. (1835) plt. 2, figs. 11, 12. NYST, 1871: 95 [as *Acirsa* "Beck"]. TRYON, 1887: 80. DALL, 1889: 308 ["Beck," as a synonym of *Scala costulata* (Mighels)]. DALL, 1917: 474 ["Beck"]. KEEN, (in Burch) 1945: 20. MACPHERSON, 1971: 40 ["Beck"].

Epitonium (Acirsa) borealis "(Beck)" (Lyell): DALL, 1921: 114; plt. 13, fig. 10. I. S. OLDROYD, 1927: 54; plt. 31, fig. 4 [as *boreale* "(Beck)" (Lyell)].

Epitonium (Acirsa) borealis "Gould": KEEP, 1935: 178; fig. 152 (description is for *Opalia borealis* Gould).

Epitonium boreale (Lyell): KEEN, 1937: 35. BURCH, 1945: 20. MORRIS, 1952: 87; plt. 24, fig. 6.

Turritella costulata MIGHELS & ADAMS, 1842: 50; plt. 4, fig. 20, (non BORSON, 1825). CLENCH & TURNER, 1950: 229 to 231; plt. 99, figs. 1-3 (as synonym of *Acirsa costulata* (Mighels & Adams, 1842)).

Scaloria costulata: TRYON, 1887: 80; plt. 16, figs. 10, 12, 18. MACPHERSON, 1971: 40 (as *Acirsa*). ABBOTT, 1974: 114 (as *Acirsa* and synonym of *A. borealis*).

Scaloria ochotensis MIDDENDORFF, 1849: 98; plt. 12, figs. 12-14. CARPENTER, 1857: 216, 220, 223. TRYON, 1887: 76; plt. 15, fig. 87. DALL, 1917: 474. I. S. OLDROYD, 1927: 51 as *Scala*. BURCH, 1945: 20.

Epitonium (Acirsa) ochotensis: DALL, 1921: 114.

Acirsa ochotensis: ABBOTT, 1974: 114 (as synonym of *A. borealis*).

Description of *Acirsa borealis* (Lyell): "Whitish or greyish fulvous, thick; whorls 8, slopingly, slightly convex, with a spiral rib below, upper portion more or less distinctly longitudinally ribbed, gradually fading until the body whorl is smooth or nearly so. Length 18-22 mill." (from TRYON, 1887: 80).

Additional Description: Shell brownish in color, thin, elongate, turreted; nuclear whorls 2, smooth; remaining whorls 9 or 10; suture definite but not impressed; axial sculpture of low ribs which continue to the suture but do not join the ones above, sometimes obsolete from the penultimate whorl down to the basal disk; spiral sculpture of about 15 striae, sometimes brown in color; basal disk strong, elevated, beyond which the axial costae do not extend; aperture round, slightly patulous anteriorly; operculum chitinous, paucispiral. Length, 19 to 60 mm; width, 6 to 20 mm.

Type Material and Type Localities:

Scaloria borealis Lyell: Holotype from Uddevalla, Sweden, lost. Hypotypes MCZ no. 187118, from Greenland.

Turritella costulata Mighels and Adams: Holotype from Massachusetts, lost (R. I. Johnson, 1949): Neotype MCZ no. 165598, from Georges Bank, Massachusetts.

Scaloria ochotensis Middendorff: Holotype in Museum of St. Petersburg (Leningrad), Russia; from south coast of Sea of Okhotsk.

Distribution, Ecology and Bathymetric Range: Circumboreal; in the Atlantic, from Massachusetts north to Nova Scotia, and Greenland; in the northern Pacific, Sea of Okhotsk and the Aleutian Islands, Alaska. Little is known of the ecology of this species. It occurs at least from low water to a depth of approximately 90 m. [For a complete summary of stations on the Atlantic seaboard see CLENCH & TURNER (1950: 230, 231).]

Geologic Record: Pleistocene to Recent. Pleistocene occurrences of this boreal species are few, at least in the northeastern Pacific. ALLISON (1973: 20) has reported it from the Pleistocene of Amchitka Island in the Bering Sea.

Discussion: LYELL (1835) figured an unnamed *Turritella* sp. in a list of fossils from Uddevalla, Sweden. In 1841 he validated the specific name *Scaloria borealis* when he cited the previous figure of *Turritella* sp. [See ICZN Code, Art. 16 (vii)]. There has been confusion over the exact date of Lyell's paper because the Transactions of the Geological Society of London were published in two parts; Part 1, containing the paper read by Lyell in 1839, was published in 1841, Part 2 was published in 1842. Beck has sometimes been given credit for the name, but did not publish it. LYELL (1841: 136) gave him credit for supplying a number of names.

Turritella costulata is not only a synonym of Lyell's taxon but also a homonym of Borson, 1825.

Scaloria ochotensis is another synonym of *Acirsa borealis*, although because of its large size (60 mm), Middendorff thought it to be distinct.

Acirsa cerralvoensis (DuShane, 1970)

(Figure 2)

Epitonium (Acirsa) cerralvoensis DuShane, 1970: 3; fig. 3. Sphon, 1970: 10.

Acirsa cerralvoensis: Keen, 1971: 436; fig. 666. DuShane, 1974: 49, 50; fig. 60.

Epitonium (Asperiscala) cerralvoensis: Abbott, 1974: 123 ("an *Acirsa*?").

Original Description: "Shell of medium size, tall and slender, thin but strong, light brown in color, with 10-12 gradually enlarging, rounded whorls, two opaque nuclear whorls; suture moderately impressed; axial ridges pale brown, 16 on the fourth whorl, gradually becoming obsolete on succeeding whorls, spiral ridges wider than the interspaces, 19 on last whorl; peritreme incomplete, lip

thin, columella arched; no basal ridge; operculum horn colored, paucispiral. Dimensions (in mm): length 11.8; width 3.7 (holotype)." (DuSHANE, 1970: 3).

Additional Description: A species with a slender, pale brown shell, differing from other Panamic-Galapagan epitoniids in having reduced axial costae and unevenly spaced spiral striae. Length, 11 to 16 mm; width, 3.7 to 4.2 mm.

Type Material and Type Locality:

Epitonium (Acirsa) cerralvoensis DuShane: Holotype LACM no. 1200; paratype LACM no. 1201; west side of Cerralvo Island, Baja California Sur, Gulf of California, Mexico.

Distribution, Ecology and Bathymetric Range: West side of the Gulf of California south to Cape San Lucas, Baja California Sur, Mexico, occurs on sand substrate in from 7 to 38 m.

Geologic Record: Pliocene, Recent.

Upper Pliocene: San Diego Formation, hill southwest of Goat Canyon, southwestern-most San Diego County, LACMIP loc. 305 [1].

Recent: Specimens in the LACM Collection are all from the Gulf of California, Mexico; 1 specimen off Puerto Refugio, Angel de la Guarda Island (AHF 1051-40) in 38 m; 2 specimens west side, Cerralvo Island (LACM Nos. 1200 and 1201) in 13 m; 1 specimen off Rancho Palmilla (LACM 66-17), in from 18 to 36 m; 1 specimen Pulmo Bay (LACM 66-20), in 7 m; 1 specimen off Punta Arena (LACM 66-21), in from 18 to 36 m; 1 specimen off Cape San Lucas (LACM 66-14), in from 18 to 36 m.

Discussion: Modern occurrences of this species are rare. Lengths of known specimens vary from 11 to 16 mm and widths from 3.7 to 4.2 mm. As a fossil this species is known only from the upper Pliocene, in the southwestern-most portion of San Diego County, California.

Amaea Adams & Adams, 1853

[Type species (SD, DeBOURY, 1909): *Scalaria magnifica* Sowerby, 1844]

Shells white, yellow-brown or dark brown; whorls joined; axial sculpture strong or weak, usually forming rectangles within which are extremely fine threads; sculpture below basal ridge similar to that above.

Subgenus *Scalina* Conrad, 1865;

synonym *Ferminoscala* Dall, 1908

[Type species (SD, PALMER, 1937): *Scalaria staminea* Conrad, 1865]

Sculpture below basal ridge or keel different from that above.

The northern limit in the eastern Pacific of the genus *Amaea* and subgenus *Scalina*, previously thought to be the Holocene of Cedros Island, Baja California Norte, Mexico, is extended to the Pleistocene of southern California (see *A. (S.) effiae*).

Amaea (Scalina) brunneopicta (Dall, 1908)

(Figures 3, 4)

Epitonium (Ferminoscala) brunneopictum DALL, 1908: 316; pl. 8, fig. 10. BOSS, *et al*, 1968: 51.

Epitonium brunneopictum: DALL, 1917: 474. STRONG, 1945: 21. CLENCH & TURNER, 1950: 287, as (*Scalina*).

Scalina ferminiana brunneopicta: KEEN, 1958: 278.

Amaea (Scalina) brunneopicta: KEEN, 1971: 436; fig. 670.

DuSHANE, 1974: 53, 54; figs. 63, 64. ABBOTT, 1974: 117.

? *Eglisia nebulosa* DALL, 1919: 348. BOSS *et al*, 1968: 218.

Eglisia (?) nebulosa: KEEN, 1958: 277; fig. 155.

Eglisia nebulosa: KEEN, 1971: 436; fig. 670 (as synonym of *A. brunneopicta*). DuSHANE, 1974: 53; fig. 64 (as synonym of *A. brunneopicta*).

Englisia [sic] nebulosa: ABBOTT, 1974: 117 (as synonym of *A. brunneopicta*).

Original Description: "Shell slender, acute, pale brownish, with broad peripheral band and basal disk of darker brown, and about 11 whorls, exclusive of the (lost) nucleus; sculpture of the same type as in the preceding species [*Epitonium (Ferminoscala) ferminianum* Dall, 1908] with, between the sutures, 4 primary and about 6 secondary spirals beside the spiral striae; the axial lamellae are very small and sharp, regularly spaced, little raised and about 36 on the penultimate whorl, they appear as whitish lines on a brown background; basal disk sharply spirally threaded, little raised; aperture as figured, when fully grown probably with a thick varix. Length of shell, 37 [mm], of last whorl, 14 [mm]; of aperture, 8 [mm]; diameter of basal disk, 9 [mm]; max. diameter 10 mm." (DALL, 1908: 316).

Additional Description: Shell size medium to large; slender, acute, color brown; whorls 13 to 14, convex, rounded in all stages; nuclear whorls lacking; first 2 whorls crenulated by the axial and spiral sculpture, third whorl with one strong cord at the periphery, fourth and fifth whorls with one strong cord at the periphery with a weaker one on either side, sixth whorl with 3 strong cords at the periphery with 2 weaker cords on either side, from there

on down the cords increase in number until, on the last whorl, there are 9 rounded, broader cords; sutures moderately deep; costae 25 to 40 on the last whorl, white, thin, sharp on early whorls, less sharp on later whorls; the cords intersected by the costae forming small, unevenly spaced rhomboids within which there are fine axial and spiral threads, with the axial threads crossing over the spiral cords forming the rhomboid; basal area brown, defined by a somewhat thickened cord, sculpture same as on the body whorl but fainter; lip white, thin, slightly crenulated by the spiral ribs crossing the last costa, patulous; peritreme incomplete, brownish color of the base can be seen as a brown spot anteriorly on the inside of the aperture; operculum dark brown, multispiral. Length 11 to 44 mm; width 3 to 12 mm.

Type Material and Type Localities:

Epitonium (Ferminoscala) brunneopictum DALL: Holotype USNM 97084; Cedros Island, Baja California Norte, Mexico.

? *Eglisia nebulosa* Dall: Holotype USNM 120702; Cape San Lucas, Baja California, Mexico.

Distribution, Ecology and Bathymetric Range: From Cedros Island, Baja California Norte, Mexico (approximately 28°07'N, 115°11'W), south throughout the Gulf of California, and south on the west Mexican coast to Costa Rica (10°53'45"N, 85°57'45"W). Occurs on a mud substrate, in from 9 to 72 m.

Geologic Record: Pliocene to Recent.

Upper Pliocene: San Diego Formation, southernmost San Diego County, California, LACMIP locs. 305 [1697], 305-A [12], 305-C [73], and 319 [23].

Recent Records: This is the only living species of *Scalina*

taken as far north as Cedros Island, Baja California, Mexico.

Cedros Island, Baja California Norte, Mexico (approximately 28°07'N, 115°11'W), (type locality), *Albatross* station 2835, in 10 m, one specimen (USNM 97084). Off Cabo Haro, Guaymas, Mexico (27°54'N, 110°53'W), *Ariel* expedition, several specimens, in 36 to 72 m, August 1960. Playa Blanca, Costa Rica (10°53'45"N, 85°57'45"W), *Velero* III, in 45 m, one specimen (LACM-AHF 463-35) February 1935.

Discussion: DALL (1908b: 316) erred when he surmised that *Amaea (Scalina) brunneopicta*, when fully adult, probably had a thick varix on the aperture. DALL's (1919: 348) *Eglisia nebulosa* from off Cape San Lucas, Baja California Sur, Mexico, was based on a worn specimen of *A. (S.) brunneopicta*.

Amaea (Scalina) effiae (Willett, 1939)

(Figure 8)

Alabina effiae WILLETT, 1939: 202; pl. 54, fig. 1. WILSON & BING, 1970: 6.

Alabina (?) aff. *A. effiae*: KEEN & BENTSON, 1944: 13; table 1.

Original Description: "Shell elongate-conic, white. Nuclear whorls 2, globular, smooth and shining. Post-nuclear whorls well rounded; sutures deep. Early post-nuclear whorls apparently smooth; later ones with very obscure, raised, irregularly spaced spiral lines, visible only under a lens, and varying in strength in the different specimens examined. Base of last whorl rounded and somewhat wrinkled at the columella. Imperforate. Aperture broadly

Explanation of Figures 1 to 12

- Figure 1: *Scalaria borealis* Lyell, 1841. From DALL, 1921: pl. 13, fig. 10; length, 19 mm; width, 6.5 mm × 2.9
 Figure 2: *Acirsa cerralvoensis* (DuShane, 1970). Holotype, LACM 1200; length, 11.8 mm; width, 3.7 mm × 3.6
 Figure 3: *Epitonium (Ferminoscala) brunneopicta* Dall, 1908. Holotype, USNM 97054; length, 37 mm; width, 10 mm × 1.3
 Figure 4: ? *Eglisia nebulosa* Dall, 1919. Holotype, USNM 120702; length, 19 mm, width, 6 mm × 2.7
 Figure 5: *Scalaria bellastrata* Carpenter, 1864. Holotype lost; lectotype by PALMER, 1958, USNM 14831b; length, 9 mm; width, 7 mm × 3.55
 Figure 6: *Epitonium (Asperiscala) cookeanum* Dall, 1917. Holotype USNM 211019; length, 9.5 mm; width, 4 mm × 6
 Figure 7: *Scalaria hemphilli* Dall, 1878a. Holotype, USNM 7991; length, "about an inch," DALL, 1878a; Pliocene ca. × 2.2

- Figure 8: *Alabina effiae* Willett, 1939. Holotype, LACMIP Type Collection 1061; length, 12 mm, width, 4.5 mm; Pleistocene × 4.5
 Figure 9: *Scala lowei* Dall, 1906. Holotype lost. Paratype, USNM 191548; length, 7 mm; width, 4 mm × 5.1
 Figure 10: *Epitonium (Asperiscala) tinctorium* Dall, 1919. Lectotype by DUSHANE (1974: 25), USNM 218100; length, 7 mm; width, 3 mm × 5.2
 Figure 11: *Epitonium (Scala) caamanoi* Dall & Bartsch, 1910. Type material lost. Figure after DALL & BARTSCH, 1910: pl. 1, fig. 1; length, 7 mm; width, 4 mm × 5
 Figure 12: *Nitidiscala caamanoi* (Dall & Bartsch, 1910). Specimen, LACM 36519; length, 16 mm; width, 8 mm × 3

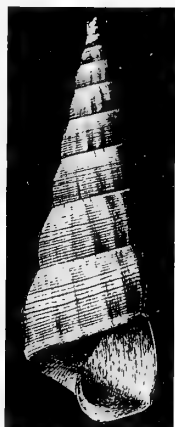


Figure 1

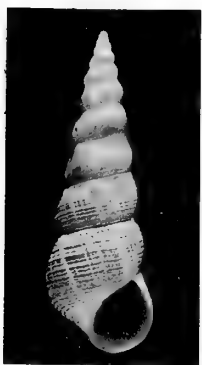


Figure 2



Figure 3



Figure 4



Figure 5



Figure 6



Figure 7

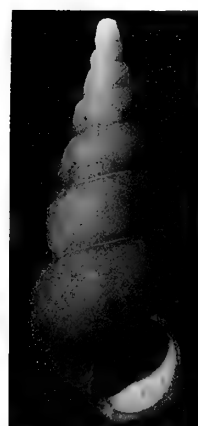


Figure 8



Figure 9

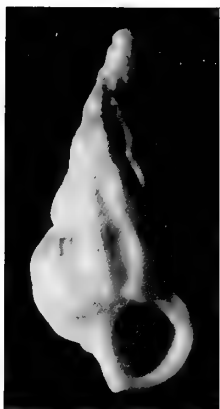


Figure 10



Figure 11

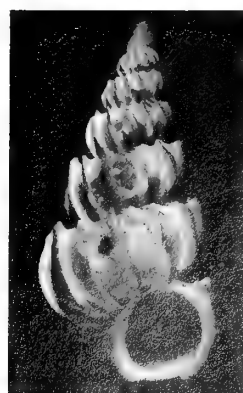


Figure 12

ovate, without trace of canal; outer lip thin, slightly reflected. Columella strongly curved; parietal wall apparently not calloused. Length, 12 mm; diameter, 4.5 mm." (WILLETT, 1939: 202).

Additional Description: Shell medium to large in size, nuclear whorls 2, smooth, remaining whorls 7 to 9, convex, rapidly increasing in size, sutures moderately deep; spiral sculpture of fine threads varying in size, irregularly spaced; costae on the final whorl weak, irregularly spaced, but forming rhomboids with the threads of the spiral sculpture, axials crossing over the spiral threads forming the rhomboids; basal sculpture apparent, but fainter; aperture oval; outer lip thin, patulous, slightly crenulated by the spiral threads crossing the last costae; peritreme incomplete. Length 12 to 18 mm; width 4.5 to 7.5 mm.

Type Material and Type Locality:

Amaea (Scalina) effiae (Willett): Holotype LACMIP 1061; Pleistocene, "Lower San Pedro series" [= Lomita Marl], Hilltop Quarry, San Pedro, California [LACMIP loc. 64]. Paratypes LACMIP 1729, 1730; Timm's Point Silt, Timms Point, San Pedro, California [LACMIP loc. 62].

Distribution: Known only as a fossil.

Geologic Record: Pleistocene.

Lower Pleistocene: Santa Barbara Formation, Packerds [Beacon] Hill, Santa Barbara (Keen and Bentson, 1944: 13; as aff.), Lomita Marl, below Park Western Drive and Host Place, San Pedro, LACMIP loc. 435 [3], and at old Hilltop Quarry [type locality], LACMIP loc. 64 [1], Timms Point Silt, Timms Point, San Pedro, California, LACMIP loc. 62 [2].

Discussion: WILLETT (1939:202) questioned the placement of his new species in *Alabina* because of its large size. His specimens, although worn, indicate a close affinity to *Amaea (Scalina) brunneopicta* (Dall), having the same fine spiral and axial sculpture and a thin lip. This species extends the known range of *Amaea (Scalina)* as a Pleistocene fossil north into southern California. J. W. Durham (personal comm., 1976) agrees with the placement of *effiae* in the genus *Amaea*.

Asperiscala DeBoury, 1909

[Type species: (OD) *Scalaria bellastrata* Carpenter, 1864] Shells white or pink to dark gray or brown; costae usually recurved, sometimes with a spine on the whorl shoulder; sculpture of heavy cords to fine striations, sometimes obsolete on the later whorls.

Asperiscala bellastrata (Carpenter, 1864)

(Figure 5)

Scalaria bellastrata CARPENTER, 1864a: 613, 660 [Reprinted, 1872: 99, 146]. CARPENTER, 1866: 221. ORCUTT, 1885: 539. TRYON, 1887: 84. COOPER, 1888: 263. DALL, 1917: 475. *Scala bellastrata*: ARNOLD, 1903: 263; pl. 9, fig. 17. ARNOLD, 1906: 36. KELSEY, 1907: 49 (as *S. bellastrata*). COSSMAN, 1912: 28; pl. 2, figs. 42, 50. DEBOURY, 1919: 34. *Epitonium bellastratum*: KEEN, 1937: 35. ABBOTT, 1974: 121; fig. 1246. KENNEDY, 1975: 27. *Epitonium (Asperoscala) [sic] bellastrata*: DALL, 1921: 114. I. S. OLDROYD, 1927: 55. *Epitonium (Asperiscala) bellastratum*: GRANT & GALE, 1931: 857. KEEP, 1935: 179. DURHAM, 1937: 489. WILLETT, 1937b: 401. STRONG, 1945: 22 (as *E. (A.) bellastrata*). BURCH, 1945: 23. SMITH & GORDON, 1948: 190. *Epitonium bellastratum*: KEEN, 1937: 35. ABBOTT, 1974: 121; fig. 1246. KENNEDY, 1975: 27. *Epitonium (Asperiscala) bellastratum [sic]*: PALMER, 1958: 189; pl. 20, figs. 25, 26 (lectotype).

Original Description of *Asperiscala bellastrata* (Carpenter, 1864a): "Shape like *pretiosa*, jun.: ribs very close, spinous at shoulder, crossed by spiral riblets."

Later Description: "S. t. tenuissima, albida; anfr. vii, valde tumentibus, haud nisi per costas attingentibus; costis circ. xvii, acutis extantibus reflexis, haud semper in spira attangentibus, postice angulatis, parum spinosis; interstitiis circa spiram basimque dense spiraliter lirulatis, lirulis rotundatis, super varicum angulum obsoletis; apertura ovata, umbilico magno. Long. 0.78, long. spir. 0.55, lat. 0.38; div. 40." (CARPENTER, 1866: 221).

Additional Description: Shell turreted, with elevated spire; nuclear whorls 3, smooth, opaque white, fourth whorl showing axial and spiral sculpture, remaining 5 to 6 whorls rapidly enlarging, very convex; suture deep; costae 15-17, reflected and with a sharp spine at the shoulder, dipping into the suture and joining the next costae above; spiral sculpture clearly defined by 20-25 ribs, interspaces slightly narrower; umbilicus large, aperture oval with reflected margins resting on 2 costae posteriorly, with a spine at the posterior margin; operculum, very dark brown, horny, paucispiral. Length 3 to 20 mm; width 2.33 to 11 mm.

Type Material and Type Locality:

Scalaria bellastrata (Carpenter): Syntypes from southern California lost (fide PALMER, 1958: 190). Lectotype by PALMER, 1958 (USNM 14831b); Monterey, California.

Distribution, Ecology and Bathymetric Range: Middle Farallon Island, San Francisco County, California (37°

48' N, 122°59' W), south to the U.S.-Mexican border (32°30' N, 117°09' W). Apparently feeds on sea anemones. Dredged in from 18 to 103 m, on mud or sand substrate.

Geologic Record: Pliocene, Pleistocene, Recent.

Upper Pliocene: Fernando Formation, Sixth and Hope Streets, downtown Los Angeles, LACMIP loc. 466 [3 f.], Cherry Avenue and Interstate 405, Long Beach, LACMIP loc. 423 [25] (KENNEDY, 1975: 27).

Lower Pleistocene: Lomita Marl, below Park Western Drive and Host Place, San Pedro, LACMIP loc. 435 [1]. Timms Point Silt, Timms Point, San Pedro, LACMIP loc. 130-7 [1].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP locs. 59 [343] (WILLETT, 1937: 401), and 61 [1]. Deadman Island, San Pedro, LACMIP loc. 2 [2]. East bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-2 [10] (KANAKOFF & EMERSON, 1959: 27), and 66-1 [2]. Newport Mesa, west side of "middle" Newport Bay, LACMIP loc. 68-B [specimens missing] (KANAKOFF & EMERSON, 1959: 27).

Recent Records: Northeast of Middle Farallon Island, San Francisco County, California (37°48' N, 122°59' W), 67 m, on sand, August 1938, one live specimen (LACM-AHF 887-38). Abalone Point, Laguna Beach, Orange County, California, 97 to 103 m, in mud, one specimen (LACM-AHF 1131-40). Off the U.S.-Mexican border (32°30' N, 117°09' W), 41 m, March 1957, one live specimen (LACM-AHF 4910-57). Most of the recent specimens are from San Pedro to Santa Catalina Island, California, perhaps because more dredging has been done in the past from off this limited locality than from any other area.

Discussion: The types of Carpenter's species are lost (PALMER, 1958: 190). The lectotype of PALMER (1958) (USNM 14831b) from Monterey, California is a fragmented specimen of 2 remaining whorls with the outer lip partially broken, with enough remaining to show that the shell is turreted, with a reflected portion of the upper lip, deep umbilicus and clean-cut spiral sculpture; length 9 mm; width 7 mm (Figure 5). Except for CARPENTER's (1866) Latin description, no complete description or diagnosis has been published.

Off the southern California coast some interesting observations have been made among the artificial reefs made up of old street cars and automobiles. An Associate Marine Biologist for the State of California, the late Charles H. Turner (personal communication, 1968), SCUBA diving offshore from Santa Monica and Hermosa Beaches, California, among the man-made reefs, at 18 m depth, photo-

graphed purple pile perch (*Rhacochilus vacca*). On examining the stomach contents he discovered that the fish had been feeding on *Asperiscala bellastrata*. All of the fish examined had absorbed the snail's purple dye into their flesh, effecting a violet-purple hue to the fish, readily observable under water. This is the first reported instance of the penetrating influence of the snail's dye into the flesh of a fish, apparently with no ill effects upon the fish.

Asperiscala cookeana (Dall, 1917)

(Figure 6)

Epitonium (Asperiscala) cookeanum DALL, 1917: 475. BAKER, HANNA & STRONG, 1930: 51; pl. 3, fig. 3. BURCH, 1945: 23. KEEN, 1958: 271. KEEN, 1971: 424; fig. 165. DUSHANE, 1974: 11, 12; fig. 8. ABBOTT, 1974: 123.

Epitonium (Asperoscala) [sic] cookeana: DALL, 1921: 114.

Epitonium cookeanum: I. S. OLDROYD, 1927: 56. KEEN, 1937: 35. BOSS, et al, 1968: 89.

Epitonium (Asperiscala) cookeana: STRONG, 1945: 22.

Original Description: "Shell small, pink, solid, acute, imperforate, the nucleus lost, with eight well rounded subse-quent whorls; with 10 rather solid, smooth, continuous white varices making less than half a turn round the spire; spiral sculpture of extremely fine uniform threads covering the whorl between the varices; the terminal varix thicker than the others; all the varices broader at the inter-section with the suture but not spinose. Length, 9.5 mm; diameter, 4 mm." (DALL, 1917: 475)

Additional Description: Shell small, white, sometimes with a pinkish cast between the costae; nuclear whorls 3, small, brown, glassy; later whorls 8, rounded; costae 10 to 12, solid, white, smooth, heavier at the suture, not re-flected; spiral threads between costae fine; suture deep; umbilicus lacking; aperture round; outer lip heavy, thin-ner parietally. Length 7 to 10 mm; width 3 to 5 mm.

Type Material and Type Locality:

Epitonium (Asperiscala) cookeanum DALL: Holotype USNM 211019. Named in honor of Miss J. M. Cooke of San Diego on the basis of one specimen obtained for her, presumably from La Paz, by Capt. Porter.

Distribution, Ecology and Bathymetric Range: La Jolla and San Diego, California (approximately 32°40' N, 117°20' W), to La Paz, Baja California Sur (24°15' N, 110°15' W), and Espiritu Santo Island, Gulf of California, Mexico (24°30' N, 110°15' W). Nothing is known of the habitat of this species.

Geologic Record: Pliocene, Recent.

Upper Pliocene: San Diego Formation, in southwestern-

most San Diego County, California, LACMIP loc. 305-C [1].

Recent Records: La Jolla, California, one specimen (DuShane Collection). Ocean Beach, San Diego County, California, one specimen (SDNHM 43661). Magdalena Bay, Baja California Sur, Mexico, collected by Orcutt, 1917, eight specimens, depository unknown. Cape San Lucas, Baja California Sur, Mexico, collected by McLean, 1966, one specimen (LACM 66-13). Espiritu Santo Island, Gulf of California, Mexico, one specimen (CAS).

Discussion: This is a rare species about which we know little. All of the modern records are of dead specimens, taken intertidally.

Asperiscala hemphilli (Dall, 1878)

(Figure 7)

Scalaria hemphilli DALL, 1878a: 12, 16. DALL, 1878b: 29. COOPER, 1888: 263. ARNOLD, 1903: 28, 44, 264. DEBOURY, 1919: 35. BOSS, *et al.*, 1968: 155.

Scala hemphilli: ARNOLD, 1906: 36.

Epitonium hemphilli: DALL, 1917: 472.

Epitonium (Boreoscala) hemphilli: GRANT & GALE, 1931: 856.

Epitonium (Asperiscala) hemphilli: DURHAM, 1937: 481, 490; pl. 56, fig. 856.

Original Description: "Shell in general resembling a robust specimen of *S. indianorum*, having from nine to twelve varices on the last whorl, coronated behind near the suture, wholly pure white; surface of the whorls beneath the varices longitudinally delicately sculptured, with alternate riblets and grooves. Length about an inch; apical angle about 30°.

This species has the sculpture of *S. bellastriata*, but the shape of *S. indianorum*, and is the only grooved species, except the former, which has yet been reported from this region. All the specimens are decollate." (DALL, 1878: 16.)

Additional Description: Shell large in size, heavy looking; nuclear whorls lost, remaining whorls about 6, with fine spiral sculpture and equally fine interspaces; costae 10 to 11, varying from narrow to wide, strongly reflected with an angulation at the shoulder; suture not deep; non-umbilicate; aperture oval, reflected, resting on the costae which continue to the base; outer lip thickened by the last costa. Length 13 to 22 mm; width 7 to 10 mm.

Type Material and Type Locality:

Scalaria hemphilli Dall: Holotype USNM 7991; San Diego Formation, Balboa Park, San Diego, California (Pliocene).

Distribution and Ecology: Extinct; known only from southern California as a fossil.

Geologic Record: Pliocene; Pleistocene (?).

Upper Pliocene: Niguel Formation, Via La Mirada, San Juan Capistrano, LACMIP loc. 4922 [1]. San Diego Formation, Pacific Beach, LACMIP loc. 4847 [1], Pacific Beach, at end of Arroyo Drive, LACMIP loc. 107 [9], and in southwesternmost San Diego County, LACMIP loc. 305 [4].

Discussion: This species was described at an early date (DALL, 1878a: 16) but was not figured (see Figure 7). Dall compared *Asperiscala hemphilli* to a robust *Nitidiscala indianorum* with the spiral sculpture of *Asperiscala bellastriata*, each of which has a different shell. DALL (1917: 472) later compared his species to *Boreoscala greenlandica*, which it does not resemble.

Asperiscala hemphilli has been reported in the Pleistocene upper San Pedro Series [= Palos Verdes Sand] (ARNOLD, 1903: 44, 264), and Pliocene San Diego Formation (ARNOLD, 1906: 36). *Asperiscala hemphilli* seems to be restricted to the southern California area, with few specimens extant.

DURHAM (1937: 490) suggested that *A. hemphilli*, *A. clarki*, and *A. bellastriata* are closely related. DUSHANE (1974: 20, 21) synonymized *A. clarki* with *A. minuticosta* (DeBoury). *Asperiscala hemphilli* differs from *A. bellastriata* by having a more slender shell, fewer costae (10 or 11), finer spiral sculpture, no umbilicus and from *A. minuticosta* by having less swollen whorls, heavier costae with a blunter spine at the shoulders, no umbilicus, and a shallower suture.

Asperiscala lowei (Dall, 1906)

(Figure 9)

Scala lowei DALL, 1906: 44. KELSEY, 1907: 49. BOSS, *et al.*, 1968: 191.

Epitonium lowei: DALL, 1917: 475. I. S. OLDROYD, 1927: 56; pl. 31, fig. 1. KEEN, 1937: 35.

Epitonium (Asperoscala) [sic] lowei: DALL, 1921: 114; pl. 6, fig. 11.

Epitonium (Asperiscala) lowei: STRONG, 1945: 22. KEEN, 1971: 426; fig. 623. ABBOTT, 1974: 123; fig. 1290. DUSHANE, 1974: 18-20; figs. 42, 157.

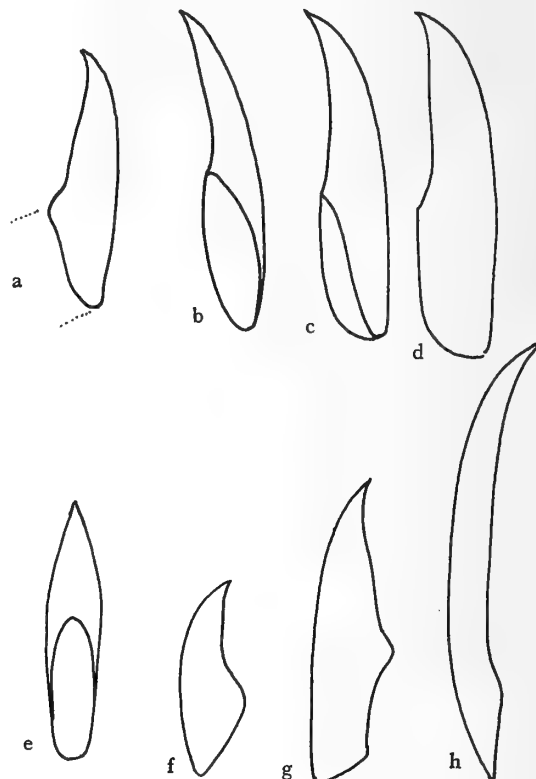
Epitonium (Asperiscala) cf. E. (A.) lowei: BERRY, 1956: 153; fig. 1.

Original Description: "Shell small, conic, with five or more rapidly increasing whorls after the (lost) nucleus; color white, whorls very convex, with deep sutures and a small spiral umbilicus; there is no basal disk or cord; sculp-

ture of about twenty-seven rather thick, strongly reflected, smooth, close-set varices, and very close, fine spiral threads, covering the whorl between the varices, and separated by about equal sulci; aperture sub-circular, slightly higher than wide, the reflected margin wide at the outer lip, patulous at the inner base, narrow between the shoulder and the preceding whorl, and at the shoulder produced into a short, rather stout spine which, repeated on successive varices, coronates the whorls. Length (without nucleus), 7.0 mm, diameter, 4.0 mm." (DALL, 1906: 44).

Additional Description: Shell medium in size, white, conic; nuclear whorls 4, white, in most cases the fourth nuclear whorl showing fine axial costae, with here and there a heavier one; teleoconch of 5 to 9 whorls, rapidly enlarging, convex; costae 25 to 32, strongly reflected, with occasionally a heavier one, with a spine at the whorl shoulder on all costae; raised spiral ridges between costae, unevenly spaced, forming rectangles within which are 2 fine horizontal threads (magnification $\times 40$); sulci twice the width of the ridges; suture deep; umbilicus deep, spiral; aperture oval; lip thin, patulous at base, reflected, with a pointed

spine at the shoulder; operculum dark brown, horny, thin, and paucispiral. Length, 3 to 25 mm; width, $1\frac{1}{2}$ to 9 mm. The radula is rectangular, with compressed, conical, horn-like teeth, about 20 in one row (Figure 69). The radular slide is at the SDNHM; the specimen from which it was



(adjacent column →)

Figure 69

Asperiscala lowei (Dall, 1906)

Specimen showing about 20 compressed conical uncini in the row (DuShane Collection). a: area of attachment; b-c-d: tooth revolved from lateral to $\frac{3}{4}$ view; e: tooth seen from attachment area; f: tooth from central area of ribbon; g: tooth from outer area of ribbon; h: orientation of tooth uncertain

Explanation of Figures 13 to 24

- Figure 13: *Scala (Viciniscala) minuticosta* DeBoury, 1912. Holotype: Zool. Museum Berlin, East Germany, no. 2578 (fide R. Kilias. Univ. Berlin). Photograph after DeBoury, 1912, Journ. Conchyl. 60 (2): plt. 7, fig. 1; length, 35 mm; width 17 mm $\times 2.4$
- Figure 14: *Epitonium cedrosensis* Jordan & Hertlein, 1926. Holotype, CAS(GTC) 2116, Pliocene; length, 8.5 mm; width, 3.75 mm $\times 6.5$
- Figure 15: *Epitonium dallasi* Jordan & Hertlein, 1926. Holotype, CAS(GTC) 2122; Pliocene; length, 7 mm; width, 4 mm $\times 9$
- Figure 16: *Epitonium clarki* T. S. Oldroyd, 1921. Holotype, SU 5948 [now at CAS(GTC)]; Pleistocene; length, 19 mm; width, 8 mm $\times 2.5$
- Figure 17: *Epitonium densicathartum* Dall, 1917. Holotype, US NM 111209; length, 17 mm; width, 7.5 mm $\times 2.8$
- Figure 18: *Boreoscala greenlandica* (Perry, 1811). Greenland. From PERRY, 1811: plt. 28, fig. 8

- Figure 19: *Boreoscala greenlandica* (Perry, 1811). Queen Charlotte Islands, B. C., Canada, from 146 m, rock and sand substrate, collected by Bernard and Quayle, October, 1966; length, 39 mm; width, 14 mm (DuShane Collection) $\times 3$
- Figure 20: *Boreoscala greenlandica smithi* (MacNeill, 1943). Holotype, USNM 499037; length, 14.6 mm; width, 8 mm; Pliocene $\times 3$
- Figure 21: *Scalaria polita* Sowerby, 1844 (after SOWERBY, 1844). Holotype presumably lost; not found at BM(NH) by M. Keen in 1965. No dimensions given
- Figure 22: *Epitonium (Nitidiscala) pedroanum* Willett, 1932. Holotype, LACM 1036; length, 11.7 mm; width, 3.7 mm $\times 4.7$
- Figure 23: *Epitonium implicatum* Dall & Ochsner, 1928. Holotype, CAS(GTC) 2932; length, 18 mm; width, 6 mm $\times 3.5$
- Figure 24: *Epitonium appressicostatum* Dall, 1917. Syntype, US NM 59334; length, 14 mm; width, 4.5 mm $\times 4.5$



Figure 13



Figure 14



Figure 15



Figure 16



Figure 17



Figure 18



Figure 19



Figure 20



Figure 21



Figure 22

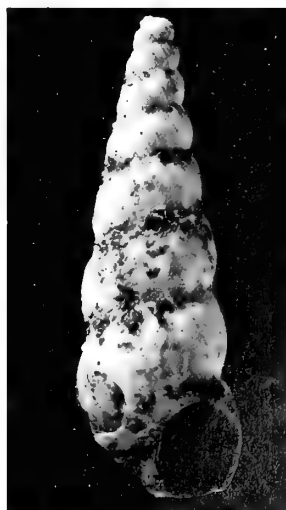


Figure 23



Figure 24

taken is in the DuShane Collection, from Bay of Los Angeles, Gulf of California, Mexico.

Type Material and Type Locality:

Asperiscala lowei (Dall): Holotype lost (Lowe Collection). Paratype, USNM 191548; dredged off Avalon, Santa Catalina Island, California.

Distribution, Ecology and Bathymetric Range: From Anacapa Island, California ($34^{\circ}02'N$, $119^{\circ}21'W$), south to Magdalena Bay, Baja California Sur, Mexico ($24^{\circ}32'30''N$, $112^{\circ}01'10''W$) with many intermediate stations; sparingly into the Gulf of California, Mexico south to Panama. Dredged from gravel, shale, sand and rock substrate in 25 to 171 m depths.

Geologic Record: Recent.

Recent Records: Northeast of Anacapa Island, California ($34^{\circ}02'N$, $119^{\circ}21'W$), dredged by *Velero* III (1938), 81 m, on rock, one specimen (LACM-AHF 876-38). Rompiente Point, Baja California Sur, Mexico, collected by McLean and LaFollette (*Searcher* 265), 1971, 90 m, shale and gravel substrate, two specimens (LACM 71-168). Magdalena Bay, Baja California Sur, Mexico ($24^{\circ}32'30''N$, $112^{\circ}01'10''W$), bottom sample by *Velero* III (1936), 31 m, one minute specimen (LACM-AHF 235). Three additional records indicate it ranges sparingly into the Gulf of California and south to Panama: San Pedro Martir Island, in 25 m, sand substrate (length 21 mm; width 9.25 mm (Skoglund Collection); Bay of Los Angeles, in 72 m, live-taken specimen (length 17 mm; width 9 mm) (DuShane Collection); Panama, live-taken specimen (length 5 mm; width $2\frac{1}{2}$ mm) (Shasky Collection).

Discussion: The holotype of *Asperiscala lowei* was returned to Lowe after a figure had been drawn of it, but is now missing. It is not at the San Diego Natural History Museum where the Lowe Collection is housed (*teste* RADWIN, 1972). A second specimen, with the same measurements, was sent by Lowe (DALL, 1906: 44), also from the same type locality (Avalon, Catalina Island, California), which became a paratype (Figure 9).

This taxon varies considerably in size (length 3 to 21 mm; width $1\frac{1}{2}$ to 9 mm). It resembles *Asperiscala bellastriata* (Carpenter, 1864), but has more reflected and numerous costae, with finer spiral sculpture, spaced farther apart, between costae. Both species occur offshore.

Asperiscala minuticosta (DeBoury, 1912)

(Figures 13, 14, 15, 16)

- Scala* (*Viciniscala*) *minuticosta* DeBOURY, 1912: 87; plt. 7, fig. 1. DeBOURY, 1919: 40.
Epitonium (*Asperiscala*) *minuticosta*: DUSHANE, 1974: 20-22; figs. 20-26 [contains complete synonymy].
Epitonium clarki T. S. OLDROYD, 1921: 115; plt. 5, fig. 13 [not *Dentiscala clarki* Olsson and Smith, 1951]. GRANT & GALE, 1931: 857 [as *E. (Asperiscala)*]. DURHAM, 1937: 490 [as *E. (Asperiscala)*]. WILLETT, 1937b: 401 [as *E. (Asperiscala)*]. VALENTINE & MEADE, 1961: 12.
Epitonium minuticosta: KENNEDY, 1975: 30.
Epitonium cedrosensis JORDAN & HERTLEIN, 1926: 446, plt. 30, fig. 3.
Epitonium (*Asperiscala*) *cedrosense*: GRANT & GALE, 1931: 857. DURHAM, 1937: 489.
Epitonium dallasi JORDAN & HERTLEIN, 1926: 447; plt. 30, fig. 2.
Epitonium (*Asperiscala*) *dallasi*: GRANT & GALE, 1931: 857. DURHAM, 1937: 489.

Original Description of *Asperiscala minuticosta* (DeBoury): "S. testa alba, tenuis, paulum translucens, sat fragilis, elongata-conica, anguste sed profunde umbilicata, sutura sat obliqua, angusta et omnino disjuncta; anfract. summis costarum tantum commissi. Anfract. embryonales deficientes. Sequentes 6, valde convexi costis mediocriter obliquis, sat distantibus, tenuibus, acutis, vix prominuis ornuli. Transversim nonnullae striae spirales, sat crebre dispositae adsunt. Ult. anfract. costis 21 munitus. Basis convexa, funiculo circumbasati omninodestituta. Columella funiculo nullo firmata. Apertura rotundata. Peristoma internum continuum et foliaceum. Peristoma externum tenue. Long. 35 mm, diam. maj. 17 mm. Habitat.—West Colombia" (DeBOURY, 1912: 87).

Additional Description: Shell medium to large, horn color or white, nuclear whorls 3, brown, glassy, conic; body whorls 7 to 8, well-rounded; suture deep; costae 13 to 21, white, reflected, with wide interspaces, true varices at irregular intervals, short, sharp spine in front of suture; spiral sculpture of about 20 sharp threads on the last whorl, with wider interspaces in which are about 8 axial striae crossing the threads between the costae and about 5 horizontal striulae within each rectangle; with a smooth space in front having no sculpture other than the costae and the axial striae, repeated around the narrow but deep umbilicus; aperture oval; reflected lip continuous, free from the costae, with a sharp spine; operculum horny, dark brown, paucispiral. Length 3 to 35 mm; width $1\frac{1}{2}$ to 17 mm.

Type Material and Type Localities:

Scala (*Viciniscala*?) *minuticosta* De Boury: Holotype, Zoologisches Mus. Berlin, East Germany, no. 2578 (*vide* R. Kilias pers. comm. 1978), Univ. Berlin: West Colombia.

Epitonium clarki T. S. Oldroyd: Holotype, SU 5948 (now at CAS); Santa Monica, California. Pleistocene.

Epitonium cedrosensis Jordan and Hertlein: Holotype CAS (GTC) 2116. Paratypes CAS (GTC) 2117-2120; Bernstein's Abalone Camp, Cedros Island, Baja California Norte, Mexico. Pliocene.

Epitonium dallasi Jordan and Hertlein: Holotype CAS (GTC) 2122; Turtle Bay, Baja California Sur, Mexico. Pliocene.

Epitonium nesioticum Dall & Ochsner. Holotype CAS (GTC) 2928; Paratypes CAS (GTC) 2929, 2930, 2931; Isla Isabela (Albemarle Island), Galápagos Islands, Ecuador. Pleistocene.

Distribution, Ecology and Bathymetric Range: Southern California (fossil), Cedros Island, Baja California Norte, Mexico (fossil and recent), south to Magdalena Bay (recent), east side Gulf of California (recent), west coast of Mexico (recent), Galápagos Islands, Ecuador (recent and fossil). Dredged on sand and broken shell substrate in 18 to 137 m.

Geologic Record: Pliocene to Recent.

Upper Pliocene: Niguel Formation, Via La Mirada, San Juan Capistrano, LACMIP locs. 4923 [2 f.], and 4925 [6 f.]. San Diego Formation, in San Diego, at end of Arroyo Drive, Pacific Beach, LACMIP loc. 107 [9], and at Euclid Avenue and Market Street, LACMIP loc. 485 [6], in southwesternmost San Diego County, LACMIP locs. 305 [483], 305-A [230], 305-B [7], 305-C [487], 318 [9], and 319 [14]; and in Baja California Norte, 4½ miles south of International border, on old coast highway, LACMIP loc. 449 [4]. Salada Formation, south side of Bahía Tortugas, Baja California Sur, LACMIP loc. 962 [1 f.].

Lower Pleistocene: Lomita Marl, below Host Place and Park Western Drive, San Pedro, LACMIP loc. 435 [1].

Upper Pleistocene: Long Wharf Canyon [= Potrero Canyon], near Santa Monica, LACMIP loc. 2670 [3]. Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP locs. 59 [240] (WILLETT, 1937b: 401; as *E. (A.) clarki*), and 5171 [1], Vermont Avenue and Sepulveda Boulevard, west of Carson, LACMIP loc. 147 [1]. Formation uncertain, in San Pedro, on Gaffey Avenue, LACMIP loc. 227 [46], and at Pacific Avenue and Oliver Street, LACMIP loc. 131 [6]. Long Beach, west of Interstate 405 and Cherry Avenue, LACMIP loc. 424 [3]. Palos Verdes Sand, on Pacific Coast Highway between Sev-

enth and Colorado Streets, LACMIP loc. 4568 [1 f.] (KENNEDY, 1975: 30). East Bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-2 [27] (KANAKOFF & EMERSON, 1959: 27; as *E. clarki*), 66-1 [20]. Newport Mesa, west side of Newport Bay, LACMIP loc. 68-B ["36," specimen missing] (KANAKOFF & EMERSON, 1959: 27; as *E. clarki*). Pacific Coast Highway, below Newport Heights, Newport Beach, LACMIP loc. 241 [1].

Discussion: For a complete synonymy of Panamic-Galapagan occurrences see DUSHANE (1974: 20-22, figs. 20-26). This is a commonly dredged species in the Panamic-Galapagan area. It has been named and renamed, both as a fossil and as a Recent species, but DeBoury is the earliest author. T. S. OLDROYD (1921: 115) named and described a Pleistocene fossil from Santa Monica, California as *Epitonium clarki* (length 19 mm; width 8 mm) (Figure 16). His description includes the characteristic fading of sculpture adjacent to the sutures, the short, sharp spines on the costae and the deep umbilicus. JORDAN & HERTLEIN (1926: 446, 447) described two Pliocene fossils from Baja California Norte (outer coast) as *E. cedrosensis* (length 8½ mm; width 3¾ mm) (Figure 14), from Bernstein's Abalone Camp, Cedros Island; and *E. dallasi* (length 7 mm; width 4 mm) (Figure 15), from 1.6 km southeast of Turtle Bay. Four whorls remain of each of the holotypes. They show the rounded whorls, with definite spiral sculpture, reflected costae, although badly worn, and the pointed spine just short of the suture, the typical umbilicus, and the heavy outer lip with the spine at the top of the aperture. Both *E. cedrosensis* and *E. dallasi* are well within the range of variability of *Asperiscala minuticosta*. Fossil occurrences of *A. minuticosta* north of Cedros Island, Baja California Norte, are extralimital for the Pleistocene and Pliocene of southern California. One live specimen of this taxon was taken by the Allan Hancock Expeditions (*Velero III*), off Cedros Island (LACM-AHF 1705-49).

Asperiscala tinctoria (Dall, 1919)

(Figure 10)

Epitonium (*Asperoscala*) [*sic*] *tinctorium* DALL, 1919: 340. LOWE, 1932: 113; plt. 9, fig. 6. BOSS, *et al.*, 1968: 320.

Epitonium (*Asperiscala*) *tinctorium*. STRONG, 1945: 22, 23. KEEN, 1958: 272; fig. 97. KEEN, 1971: 428; fig. 629. DUSHANE, 1974: 24; figs. 12, 18.

Original Description: "Shell small, white, with a narrow purple-brown spiral line in front of the suture, of six or more whorls excluding the (lost) nucleus; the whorls adjacent, the axis imperforate, with 11 to 12 varices which

about half encircle the spire; the varices smooth, slightly reflected, wider where they cross the rather deep suture; there are no varical angles or spines; the whorls are uniformly finely striated; aperture rounded; there is no basal disk or cord; no operculum was taken with the specimen; height of shell, 7; of last whorl, 3; diameter, 3 mm." (DALL, 1919: 340).

Additional Description: Shell small, yellowish-brown, with white costae; nuclear whorls 3, white, glassy; post nuclear whorls 8 or 9, rapidly enlarging; costae 8 to 12, slightly reflected, showing growth lines, thicker on the body whorl; spiral threads unevenly spaced between whorls; suture fairly deep; with a purple-brown band on the whorls near the suture; aperture round; shell imperforate; lip slightly patulous at bottom; operculum brown, horny, thin. Length, 2 to 8.5 mm; width, 1 to 4.5 mm.

Type Material and Type Locality:

Epitonium (Asperoscala) [sic] tinctorium DALL: Lectotype, USNM 218100 by DUSHANE (1974: 25); four paralectotypes, USNM 698126 by DUSHANE (1974: 25); Magdalena Bay, Baja California Sur, Mexico.

Distribution, Ecology and Bathymetric Range: Magdalena Bay, Baja California Sur, Mexico, throughout the Gulf of California, south on the west coast of Mexico, possibly to Panama. Usually found on rubble reefs from the intertidal zone down to approximately 6 m.

Geologic Record: Pleistocene to Recent.

Upper Pleistocene: East bluff above Upper Newport Bay, Newport Beach, LACMIP loc. 136 [3]. Southeast of Punta Pequeña, outer coast of Baja California Sur, LACMIP loc. 2719 [28].

Discussion: Live-taken shells have white costae and yellowish-brown whorls, but beach specimens are white. The brown band between the costae is almost on the outer periphery of the whorl. The costae show growth lines, the spiral striations are fine and irregularly spaced between the costae, but not on them, and the lip is fairly heavy. Fresh shells are easily identified but dead shells present a problem unless these points are noted.

When DALL (1919: 340) described *Asperiscula tinctoria* he failed to choose a holotype from the 5 specimens in the type lot. DUSHANE (1974: 25) selected a lectotype (USNM 218100) that most nearly fitted Dall's description and measurements. Although collected by C. R. Orcutt many years ago, it still retains the brown band between the costae, and the fine spiral striations; the aperture is slightly damaged. The remaining 4 specimens are paralectotypes (USNM 698126).

Essentially a Panamic species, *Asperiscula tinctoria* is most frequently taken from around rocks on rubble reefs and under rocks in tide pools. On the outer coast of Baja California it is taken as far north as Magdalena Bay. Possibly because of the inaccessibility of the coast from Magdalena Bay north to Scammon's Lagoon there seem to be no records for this species, although it is quite possible for it to occur there in a shallow water habitat.

Boreoscala Kobelt, 1902

[Type species: *Turbo clathrus groenlandicus* Chemnitz, 1795 (non-binomial) (= *Scalaria greenlandica* Perry, 1811: OD Kobelt, 1902)]

Shells usually off-white, costae straplike, strongly sculptured continuing to the aperture. Whorls convex, attached, with spiral sculpture of strong ridges with deep depressions between; suture definite, but not deep; basal disk present. Aperture oval, operculum horny, black.

Boreoscala greenlandica (Perry, 1811)

(Figures 18, 19, 20)

Turbo clathrus groenlandicus CHEMNITZ, 1795: 155; plt. 195a, figs. 1878, 1879 (non-binomial).

Scalaria greenlandica PERRY, 1811: app., plt. 28, fig. 8. GOULD, 1841: 249, fig. 107 [as *S. Groenlandica*]. G. B. SOWERBY II, 1844a: plt. 34, figs. 105, 110. CARPENTER, 1857: 216, 223, 336 [as *S. groenlandica*]. DALL, 1873: 58 [as *S. grönlandicum*]. DALL, 1874: 251 [as *S. grönlandica*]. TRYON, 1887: 76; plt. 16, fig. 91 [as *S. grönlandica*]. DALL, 1921: 114. DALL, 1925: 6; plt. 22, fig. 2. I. S. OLDRYD, 1927: 349 [as *Scala grönlandica*].

Epitonium (Arctoscala) greenlandicum: KEEP, 1910: 184.

Epitonium (Boreoscala) greenlandicum: DALL, 1917: 472. GRANT & GALE, 1931: 856. KEEP, 1935: 179 [as *E. (B.) grönlandicum*].

Epitonium greenlandicum: KEEN, 1937: 35. MORRIS, 1952: 87; plt. 24, fig. 2. CLENCH & TURNER, 1952: 320; plt. 131, fig. 2, plt. 154, figs. 1-3. MACGINITIE, 1959: 83; plt. 5, figs. 2, 3. COWAN, 1964: 111. BERNARD, 1970: 81. ALLISON, 1973: 20. ABBOTT, 1974: 121, 122; fig. 1247.

Boreoscala greenlandica: HABE & ITO, 1965: 29; plt. 7, fig. 24. *Boreoscala greenlandica* "(Chemnitz)": GOLIKOV & SCARLATO, 1967: 47; fig. 35.

Epitonium (Boreoscala) greenlandicum smithi MACNEIL (in MACNEIL, MERTIE & PILSBRY, 1943), 82; plt. 11, fig. 2.

Original Description of *Boreoscala greenlandica* (Perry): "Shell of a pale brown invested with thong-shaped ribs; the four upper folds of the spire smooth; the mouth round. A native of Greenland." (PERRY, 1811: accompanying plate 28, fig. 8).

Additional Description: Shell large, pale brown or off-white; nuclear whorls 2 to 4, smooth; post-nuclear whorls 11 to 12, moderately convex, suture impressed, not deep; costae strong, curving into the suture, sometimes nearly covering the intercostal spaces, 9 to 12 on the body whorl, riding over the basal ridge, continuing to the aperture; spiral sculpture of strong ribs, 5 times the width of the deep grooves; basal ridge usually present, with about 9 regularly spaced ribs above the ridge and 3 to 5 inconspicuous ribs below; lip usually thickened, aperture subovate; operculum black, horny, with a narrow brown border. Length 11.5 mm; width 4 to 19.5 mm.

Type Material and Type Localities:

Scalaria greenlandicum Perry: Holotype lost (CLENCH & TURNER, 1952: 320); type locality restricted to Godthaab, southwest Greenland (CLENCH & TURNER, *loc. cit.*).

Epitonium (Boreoscala) greenlandicum smithi MacNeil: Holotype USNM 499037; Inner Submarine Beach, Nome, Alaska ("Pliocene" = Pleistocene).

Distribution, Ecology and Bathymetric Range: Circumboreal, Arctic Ocean near Point Barrow, Alaska, south to British Columbia, Canada; Siberia and northern Japan; taken from depths of 38 m to 163 m.

Geologic Record: Pleistocene to Recent.

Pleistocene: The species has been reported from the Pleistocene of Amchitka Island in the Aleutians by ALLISON (1973: 20), and the "Inner Submarine Beach" at Nome, Alaska by MACNEIL (in MACNEIL, MERTIE & PILSBRY, 1943: as *Epitonium (Boreoscala) greenlandicum smithi*, new subspecies; as "Pliocene"); length 14.6 mm; width 8 mm (USNM 499037) (Figure 20). MacNeil's specimen appears to be an eroded example of *Boreoscala greenlandica*, with a

broader and flatter base, and with weaker axial costae than is normal for the species.

Recent: COWAN (1964: 111), stated this species is known south to Wrangell, Alaska and off the north end of Graham Island, Queen Charlotte Islands, British Columbia, Canada; one specimen (LACM 36518) from off Point Barrow, Alaska (collected by G. E. MacGinitie, 1948); one specimen taken off the west coast of Queen Charlotte Islands, British Columbia, from 146 m, rock and sand substrate (collected by F. R. Bernard and D. Quayle, 1966) (DuShane Collection) (Figure 19).

Discussion: The early synonymy of this circumboreal species in the Atlantic Ocean is well covered by CLENCH & TURNER (1952: 320) and need not be repeated. An account of the biology of this species is given by PERRAN (1978).

Depressicala DeBoury, 1909

[Type species: (OD) *Scala aurita* Sowerby, 1844; synonym: *Pictoscala* Dall, 1917: type species (OD) *Scalaria lineata* Say, 1822 (not Röding, 1798; not Kiener, 1838)].

Shells purple-brown with low white costae and fine spiral striae that do not form a pattern, aperture oval.

Depressicala polita (Sowerby II, 1844)

(Figures 21, 22, 23, 24)

Scalaria polita SOWERBY II, 1844b: 30. SOWERBY II, 1844a: 100; pl. 34, fig. 99. REEVE, 1873: pl. 10, fig. 77. TRYON, 1887: 69; pl. 14, fig. 43. DALL, 1917: 488.
Scala polita ADAMS & ADAMS, 1853: 222.

Explanation of Figures 25 to 35

- Figure 25: *Epitonium californicum* Dall, 1917. Holotype, USNM 201202; length, 10 mm; width, 4 mm × 5
Figure 26: *Epitonium orcuttianum* Dall, 1917. Holotype, USNM 273998; length, 6.5 mm; width, 3 mm × 7.6
Figure 27: *Epitonium diegense* Dall, 1917. Holotype, USNM 211904; length, 5 mm; width, 2 mm × 4
Figure 28: *Epitonium sawinae*, variety ? *catalinense* Dall, 1917. Holotype, USNM 109502; length, 13.5 mm; width, 6 mm × 3.6
Figure 29: *Epitonium (Crisposcala) catalinae* Dall, 1908. Holotype, USNM 198628; length, 12 mm; width, 4.5 mm × 3
Figure 30: *Epitonium (Nitidoscala) tabulatum* Dall, 1917. Holotype, USNM 109569; length, 18 mm; width, 7.5 mm × 2.2

- Figure 31: *Epitonium (Nitidoscala) regum* Dall, 1917. Holotype, USNM 206596; length, 9 mm; width, 4 mm × 4.4
Figure 32: *Epitonium (Nitidiscala) contrerasi* Jordan & Hertlein, 1926. Holotype, CAS(GTC) 2121; length, 22 mm; width, 9 mm; Pliocene × 3
Figure 33: *Scalaria hindsii* Carpenter, 1856. Syntypes (2) BM (NH) 1963.21; left hand specimen designated as lectotype herein; length, 25 mm; width, 10 mm × 2.6
Figure 34: *Epitonium persuturum* Dall, 1917. Holotype, USNM 211021; length, 15.5 mm; width, 6 mm × 3.2
Figure 35: *Epitonium (Nitidiscala) cooperi* Strong, 1930. Holotype, SDMNH 345; length, 20 mm; width, 8 mm × 2.4



Figure 25



Figure 26



Figure 27



Figure 28



Figure 29



Figure 30



Figure 31



Figure 32

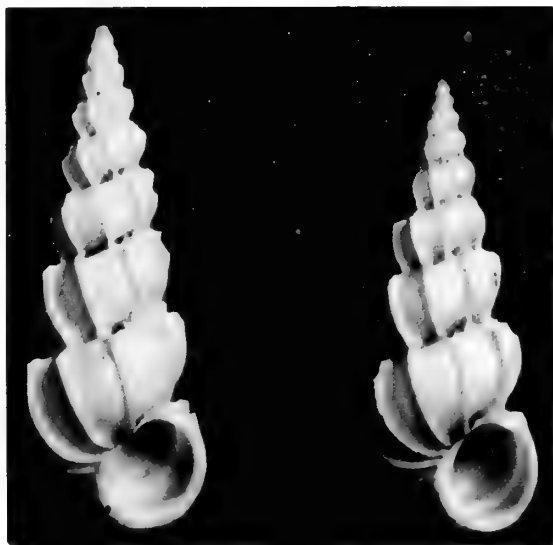


Figure 33

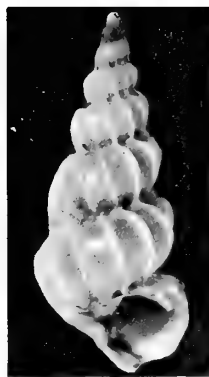


Figure 34



Figure 35

- Epitonium (Nitidiscala) politum*: KEEN, 1971: 432; fig. 655. DUSHANE, 1974: 35, 36; figs. 89-93, 96. ABBOTT, 1974: 123 (as *E. (Nitidiscala)* [sic]).
- Epitonium (Nitidoscala)* [sic] *appressicostatum* DALL, 1917: 482.
- Epitonium (Nitidiscala) appressicostatum*: STRONG, 1945: 26, 27. KEEN, 1958: 272.
- Epitonium appressicostatum*: BOSS *et al.*, 1968: 31. ABBOTT, 1974: 123.
- Epitonium implicatum* DALL & OCHSNER, 1928: 111; plt. 6, fig. 1.
- Epitonium (Nitidiscala) pedroanum* WILLETT, 1932: 88; plt. 5, fig. 3. STRONG, 1945: 27. BURCH, 1945: 30, 31.
- Epitonium pedroanum*: KEEN, 1937: 35. SPHON, 1971: 11. ABBOTT, 1974: 123.

Original Description of *Scaloria polita* Sowerby: "T. tenui, elongata, laevi, imperforata; anfractibus numerosis, vix prominentibus; varicibus sub-numerosis, tenuis, in medis anfractuum obsoletis; colore pallide griseo. The whorls are numerous, and not very prominent. The varices appear as if worn away in the centre of the whorls. Taken by Mr. Cuming at Xipixappi, West Columbia, in sandy mud, ten fathoms deep." (SOWERBY II, 1844a: 30).

Additional Description: Shell medium in size, thin, polished, yellowish brown in color; nuclear whorls 3 to 5, smooth, glassy, amber colored; post nuclear whorls 7 to 12, rounded; costae 9 to 15, white, nearly obsolete on the body whorls, slightly angulate at shoulder, continuous over suture; suture moderately deep; base rounded, non-umbilicate; aperture oval, margin slightly angular in front. Length 9 to 16 mm; width $3\frac{1}{2}$ to 5 mm (Figure 21).

Type Material and Type Localities:

- Scaloria polita* Sowerby II: Holotype presumably lost; not found at BM (NH) by M. Keen (pers. comm.) in 1965; West Colombia.
- Epitonium (Nitidoscala) appressicostatum* Dall: Lectotype USNM 678703 herein, length 14 mm; width 4.5 mm; paralectotype USNM 678703 herein, length 12 mm; width 4 mm; Acapulco, Mexico.
- Epitonium implicatum* Dall and Ochsner: Holotype CAS [GTC] 2932; Galápagos Islands, Ecuador. Pliocene (?).
- Epitonium (Nitidiscala) pedroanum* Willett: Holotype LACM 1036; paratype (1) in J. Q. Burch Collection; San Pedro, California.

Distribution, Ecology and Bathymetric Range: Catalina Island, California ($33^{\circ}27'59''$ N, $118^{\circ}36'15''$ W) south to the Galápagos Islands and Ecuador (approximately $1^{\circ}35'10''$ S, $80^{\circ}51'55''$ W). Dredged in from 11 to 393 m, rocks, nullipores, broken shells, and sandy mud substrate.

Geologic Record: Pliocene (?) to Recent.

Pliocene (?): Indefatigable Island, Galápagos Islands, Ecuador ($1^{\circ}35'10''$ S, $80^{\circ}51'55''$ W), collected by

Ochsner and Slevin, from zone "D," November 1905, one specimen, as *Epitonium implicatum* (Holotype CAS [GTC] 2932).

Recent Records: West end, Catalina Island, California ($33^{\circ}27'59''$ N, $118^{\circ}36'15''$ W), *Velero* III, 40 m, gray mud, August 1957, one specimen (LACM-AHF 5240-57). Off San Pedro, California, collected by Willett, 36 m, two specimens as *Epitonium pedroanum* (Holotype LACM 1036). Off Agua Chale, Gulf of California, Mexico, *Chamizal*, 11 m, out of starfish stomach, June 1968, one specimen (DuShane Collection). Manzanillo, Mexico, dredged by Shy, 39 m, December 1965, three specimens (DuShane Collection). Off Acapulco, Mexico (DALL, 1917: 482), 2 specimens, as *Epitonium appressicostatum* (USNM 59334). Off La Plata Island, Ecuador, *Velero* III, February 1934, 18 m, one specimen (LACM-AHF 213-34).

Discussion: This subtidal species has a wide geographic range although few records have been obtained. It is easily recognized, being the only species along the north-temperate coast to have a yellowish brown shell with white costae and a slender outline. Fresh specimens are glassy, sometimes brownish in color, the costae being mere threads. Spiral striulae mark succeeding whorls after the first 2 on some specimens. Occasionally the costae are discontinuous.

Nitidiscala DeBoury, 1909

[Type species: (OD) *Scaloria unifasciata* Sowerby II, 1844] Spiral sculpture between whorls absent.

Nitidiscala caamanoi (Dall & Bartsch, 1910)

(Figures 11, 12, 17)

- Epitonium (Scala) caamanoi* DALL & BARTSCH, 1910: 13; plt. 1, fig. 1. BOSS, *et al.*, 1968: 53.
- Epitonium caamanoi*: DALL, 1917: 482. STRONG, 1945: 24. T. S. OLDROYD, 1925: 13. I. S. OLDROYD, 1927: 62; plt. 31, fig. 3. KEEN, 1937: 35. BERNARD, 1970: 81.
- Epitonium (Nitidoscala)* [sic] *caamanoi*: DALL, 1921: 116. I. S. OLDROYD, 1924: 107; plt. 12, fig. 1.
- Epitonium (Nitidiscala) caamanoi*: GRANT & GALE, 1931: 858. STRONG, 1945: 24, 26. BURCH, 1945: 31.
- Epitonium densicathratum* DALL, 1917: 478. I. S. OLDROYD, 1927: 61. KEEN, 1937: 35. BURCH, 1945: 29. BOSS, *et al.*, 1968: 102.
- Epitonium (Nitidoscala)* [sic] *densicathratum*: DALL, 1921: 115. I. S. OLDROYD, 1924: 107.
- Epitonium (Nitidiscala) densicathratum*: STRONG, 1945: 24.

Original Description of *Epitonium (Scala) caamanoi* Dall and Bartsch: "Shell small, rather conic, white, with thirteen broadly reflexed, axially conspicuously striated varices; nucleus? (lost); whorls, more than six, varices continuous up the spire, narrow near the suture, more than doubling in width at the shoulder, where they are provided with a small spine or prominent angulation, then continuing to the base, where they are again narrowly contracted; there is no basal disk or cord, the umbilicus is closed; the surface of the whorls between the varices is smooth; the whorls are evenly rounded, and the aperture, if perfect, would probably be nearly circular. Length of six whorls (decollate), 9.5; diameter at base, 5.0, at decollation, 0.7; of aperture, 2.0 mm."

"Collected by Mr. John Macoun, No. 77a (in part), with four other species of the genus, and two dead specimens, in from 7 to 10 fathoms" (DALL & BARTSCH, 1910: 13).

Additional Description: Shell large, white, often worn looking; nuclear whorls eroded; post nuclear whorls 6 to 8, well rounded; costae 11 to 13, broadly reflected, axially striated, solid, thick, continuous from whorl to whorl, narrow near the suture, expanding on the shoulder to a small spine, remainder of costae doubling in width over the whorl, narrow at the base; surface between whorls smooth; suture distinct; aperture round, lip reflected over the costae; non-umbilicate; operculum horny, round, paucispiral. Length 9.5 to 17 mm; width 5.5 to 7.5 mm.

Type Material and Type Localities:

Epitonium (Scala) caamanoi Dall and Bartsch: Type material lost; not at Geological Survey Museum, Ottawa, Canada (pers. comm. Arthur H. Clarke, 1975); Barkley Sound, Vancouver Island, British Columbia, Canada.

Epitonium densiclathratum Dall: Holotype USNM 111209; Puget Sound, Washington, taken by the U.S. Fish Commission, station 3068, 243 m, green mud.

Distribution, Ecology and Bathymetric Range: Barkley Sound, Vancouver Island, British Columbia (50° N, 125° 20' W) Neah Bay and Puget Sound, Washington (48° N, 122° W). This is a subtidal species and good specimens are taken only by dredging in from 12 to 243 m.

Geologic Record: Pleistocene to Recent.

Upper Pleistocene: Second and Orizaba [now Beacon] Streets, San Pedro, LACMIP loc. 142 [46]. East bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-1 [1], 66-2 [5], and 136 [11]. The four Pleistocene lots indicate a southern range in earlier times than is apparent from collections of recent material.

Recent Records: Uclulet to Amphitrite Point, Vancouver Island, British Columbia, collected by C. H. Young and W. Spreadborough, 1909, one badly dam-

aged specimen (NMC 1415) 6½ whorls remain with 12 costae, length 10 mm; width 5 mm. Departure Bay, Vancouver Island, British Columbia (49° 12' N, 123° 58' W) one specimen (LACM 36519) with 8 whorls, 11 costae, length 16 mm; width 8 mm. Seiku, Washington, collected DuShane, one beach specimen, with 7 whorls, 11 costae, length 11 mm; width 5½ mm (DuShane Collection).

Discussion: The description of *Nitidiscala densiclathratum* (Dall), ex Carpenter MS (DALL, 1917: 478) agrees with that for *Nitidiscala caamanoi* and the 2 names are considered synonymous herein. The holotype of *N. densiclathratum* (USNM 111209) has 7 whorls, 11 costae, length 17 mm; width 7.5 mm. The only other lot of *N. densiclathratum* (USNM 23353) from Neah Bay, Washington, collected by J. G. Swan, has 3 broken specimens. DALL (1921: 115) gave a range from Neah Bay, Washington to San Diego, California but there are no literature citations to substantiate his southern range. *Nitidiscala caamanoi* differs from other epitoniids within the genus by having a broader shell, inflated whorls, reflected costae, narrow at the distinct suture.

Nitidiscala californica (Dall, 1917)

(Figures 25, 26, 27)

Epitonium californicum DALL, 1917: 482. I. S. OLDROYD, 1927: 62. KEEN, 1937: 35. STRONG, 1945: 25. BURCH, 1945: 31. KANAKOFF & EMERSON, 1959: 27. BOSS, *et al.*, 1968: 56.

Epitonium (Nitidoscala) [sic] californica: DALL, 1921: 116.

Epitonium (Nitidiscala) californicum: STRONG, 1930: 195; pl. 20, figs. 11, 12a, 12b. KEEN, 1958: 273. WILSON & KENNEDY, 1967: 251.

Epitonium (Epitonium) californicum: ABBOTT, 1974: 122.

Epitonium diegensis DALL, 1917: 483. KEEN, 1937: 35. BURCH, 1945: 32. BOSS, *et al.*, 1968: 104.

Epitonium (Nitidoscala) [sic] diegensis: DALL, 1921: 116.

Epitonium diegensis: I. S. OLDROYD, 1927: 63. STRONG, 1945: 26.

Epitonium (Nitidiscala) diegensis: KEEN, 1958: 274.

Epitonium (Epitonium) diegensis: ABBOTT, 1974: 123.

Epitonium orcuttianum DALL, 1917: 484. I. S. OLDROYD, 1927: 66. KEEN, 1937: 35. BURCH, 1945: 24. BOSS, *et al.*, 1968: 232.

Epitonium (Nitidiscala) orcuttiana: STRONG, 1945: 24.

Epitonium (Epitonium) orcuttianum: ABBOTT, 1974: 123.

Original Description of *Nitidiscala californica* (Dall): "Shell small, white, solid, with seven whorls and a very small brownish nucleus of a whorl and a half; varices 9 or 10, low, sharp, reflected, anteriorly axially striated, with a very small sharp spine at the shoulder; suture deep, the

whorls almost separated, rounded; base rounded, imperforate; aperture short-ovate, its inner margin resting on the preceding varices, not touching the body whorl. Length, 10.5; diameter, 4 mm. Range, San Miguel Island, California, to the Gulf of California." (DALL, 1917: 482).

Additional Description: Shell small to large in size, nuclear whorls 3, brown, glassy, the third whorl down showing faint axial sculpture; post nuclear whorls 6 to 7, well rounded, with very faint axial striations; suture deep; costae 9 to 12, reflected, with some axial growth lines crossing the whorls diagonally and before entering the very deep suture rising to a point, becoming very narrow as they enter the suture, overlapping the costa above; non-umbilicate, aperture slightly oval, lip reflected, resting on the preceding costae, with a small spine posteriorly, slightly patulous anteriorly, operculum horny, thin, brown. Average dimensions are: length 4 to 11 mm; width 2 to 4.5 mm.

Type Material and Type Localities:

Epitonium californicum Dall: Holotype USNM 201202; paratype (1) USNM 635569; San Diego, California.

Epitonium diegensense Dall: Holotype USNM 211904; paratype (1 plus fragments) USNM 635561; San Diego, California.

Epitonium orcuttianum Dall: Holotype USNM 273998; paratypes (many) USNM 635563; San Diego, California.

Distribution, Ecology and Bathymetric Range: *Nitidiscala californica* appears to be restricted in range from Newport Bay, Orange County, California (33°34'15"N, 117°30'00"W) south to Cedros Island, Baja California Norte, Mexico (28°20'25"N, 115°11'20"W). Occurs in muddy back bays, intertidally, and sublittorally to depths of 36 m.

Geologic Record: Pliocene to Recent.

Upper Pliocene: Fernando Formation, Sixth and Hope Streets, downtown Los Angeles, LACMIP loc. 466 [10]. San Diego Formation, end of Arroyo Drive, San Diego, LACMIP loc. 107 [2], southwesternmost San Diego County, LACMIP loc. 305-C [26].

Lower Pleistocene: Lomita Marl, below Park Western Drive and Host Place, San Pedro, LACMIP loc. 435 [4].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP loc. 59 [85]. Corona del Mar, LACMIP loc. 74 [1]. East bluff above Upper Newport Beach, LACMIP loc. 136 [10].

Recent Records: Newport Bay, Orange County, California, collected by A. M. Strong, five specimens (LACM 36520). Todos Santos Bay, Baja California Norte, collected by E. P. Chace, January 1926, one specimen (DuShane Collection). Cedros Island, Baja

California Norte, Mexico, collected McLean, *et al.*, RV *Searcher*, October 1971, two specimens (LACM 71-152).

Discussion: The holotype of *Nitidiscala diegensense* DALL (1917: 483), length 5 mm; width 2 mm (Figure 27), and *Nitidiscala orcuttiana* DALL (1917: 484), length 6.5 mm; width 3 mm (Figure 26), have the same characteristics as *Nitidiscala californica*. All 3 species have sharp spines, inflated whorls, and the same number of costae. All have San Diego, California as their type localities. DALL's (1917: 483) range for *N. diegensense* from San Diego to La Paz, is in error since the specimen (USNM 211507) from La Paz, Baja California Sur, Mexico, on which he based his southern record, has a more slender shell and is not related. DALL's (1917: 482) range for *N. californica*, from San Miguel Island, California to the Gulf of California, cannot be substantiated by southern specimens. It is odd that STRONG (1930), in comparing members of the genus *Nitidiscala* on the California coast, did not include a discussion of *N. diegensense* and *N. orcuttiana*.

Nitidiscala californica differs from *Nitidiscala tinctoria*, with which it has often been confused, by having a more slender shell, more reflected costae, and with a spine on the shoulders of the whorls and one on the last costa forming the lip. In addition, the costae are of a different shape. They become very narrow before entering the suture, whereas in *N. tinctoria* the costae are broad as they enter the suture.

Nitidiscala catalinae (Dall, 1908)

(Figures 29, 30, 31)

Epitonium (Crisposcala) catalinae DALL, 1908a: 252. DALL, 1917: 484. DALL, 1921: 116 (as (*Nitidoscala*)) [sic]. I. S. OLDROYD, 1927: 65. BURCH, 1945: 32. SMITH & GORDON, 1948: 191. BOSS, *et al.*, 1968: 67.

Epitonium catalinae: STRONG, 1930: 191. KEEN, 1937: 35. WILLETT, 1937a: 64. STRONG, 1945: 24. COWAN, 1964: 111. ABBOTT, 1974: 123 (as *E. (Epitonium)*).

Epitonium (Nitidoscala) [sic] tabulatum DALL, 1917: 482.

Epitonium (Crisposcala) tabulata: DALL, 1921: 116. I. S. OLDROYD, 1927: 66. BURCH, 1945: 33. SMITH & GORDON, 1948: 191.

Epitonium tabulatum: KEEN, 1937: 35. STRONG, 1945: 24. VALENTINE, 1961: 408. BOSS, *et al.*, 1968: 313. ABBOTT, 1974: 123 (as *E. (Epitonium)*).

Epitonium (Nitidoscala) [sic] regum DALL, 1917: 484.

Epitonium (Crisposcala) regum: DALL, 1921: 116. I. S. OLDROYD, 1927: 64. BURCH, 1945: 32. SMITH & GORDON, 1948: 191.

Epitonium regum: KEEN, 1937: 35. VALENTINE & MEADE, 1961: 12, 23. BOSS, *et al.*, 1968: 275. ABBOTT, 1974: 123 (as *E. (Epitonium)*).

Nitidiscala rega: STRONG, 1945: 24.

Original Description of *Nitidiscala catalinae* (Dall): "Shell slender, white, turreted, imperforate, with more than 7 adherent whorls; nucleus (lost); suture distinct, closed; varices (on the last whorl 14) continuous, making nearly one revolution around the axis in ascending the spire; they are flatly reflected, axially striate, subspinose at the shoulder, giving a tabulate aspect to the rounded whorls. There is no basal disk on the whorl, but on the basal part of each reflection of the varices there is a smooth area over which the suture travels, and which, taken collectively, gives the effect of segments of a disk imposed on the varices but not on the whorl; below the shoulder the varices are widely reflected, extending for a space to the angle of reflection of the preceding varix, where it would seem these extensions are normally attached, covering a hollow space between them and the whorl, but in the type specimen most of these extensions are broken away; aperture subcircular. Height of (decolate) six whorls, 12.0; of last whorl, 6.0; of aperture, 2.7; maximum diameter, 4.5 mm." (DALL, 1908a: 252).

Additional Description: Shell medium to large in size; off-white in color; nuclear whorls $2\frac{1}{2}$ to 3, brownish; post-nuclear whorls 7 to 12; suture distinct; costae 12 to 20, reflected, and overlapping the next costae, axially striated, often appearing chalky, angular above, tabulating the profile of the spire; lip entire, with a small spine at the shoulder formed by the last costa; non-umbilicate; operculum horny, thin, light brown, slightly oval in shape. Length 7.9 to 18 mm; width 4 to 7.5 mm.

Type Material and Type Localities:

Epitonium (*Crisposcala*) *catalinae* Dall: Holotype, USNM 198628; Catalina Island, California.

Epitonium (*Nitidoscala*) *tabulatum* Dall: Holotype, USNM 109569; Los Coronados Islands, Baja California Norte, Mexico.

Epitonium (*Nitidoscala*) *regum* Dall: Holotype, USNM 206596; Point Reyes, Marin County, California.

Geographical Distribution, Ecology and Bathymetric Range: From Forrester Island, Alaska ($54^{\circ}50'N$, $133^{\circ}32'W$) south to at least Cedros Island, Baja California Norte, Mexico ($28^{\circ}01'N$, $115^{\circ}29'W$). Occurs on sand substrate in from 29 to 110 m depths.

Geologic Record: Pleistocene to Recent.

Lower Pleistocene: Lomita Marl, below Host Place and Park Western Drive, San Pedro, LACMIP loc. 435 [64]. Timms Point Silt, in San Pedro, at Third and Mesa Streets, LACMIP loc. 99 [3], and at Timms Point, LACMIP locs. 62 [2], 130-7 [85], and 4805 [8].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP loc. 59 [2].

Recent Records: Forrester Island, Alaska ($54^{\circ}50'N$, $133^{\circ}32'W$), dredged by Willett (1914-1917), 36-72 m, one specimen. La Perouse Bank, off Barkley Sound, Vancouver Island, British Columbia, dredged by Cowan (1964), 68 to 72 m, one specimen. Northwest coast of Vancouver Island, British Columbia, dredged by Bernard (1967), 75 m, from gravel and mud, one specimen (DuShane Collection). Queen Charlotte Sound, British Columbia ($51^{\circ}54'N$, $128^{\circ}51'W$), dredged by D. B. Quayle on *G. B. Reed*, 106 m, two specimens, one live-taken (LACM 69-71). Point Reyes, Marin County, California, dredged by U.S. Fish Commission, station 4309, 110 m (USNM 206596), as *Nitidiscala regum* (Dall). Coronados Islands, Baja California Norte, Mexico, dredged by U.S. Fish Commission, station 2931, 61 m (USNM 109569), as *Nitidiscala tabulata* (Dall). Eight miles southwest of Cedros Island, Baja California Norte, Mexico ($28^{\circ}01'23'N$, $115^{\circ}29'37'W$), dredged by *Velero III* (1950), three specimens (LACM-AHF 1948-50).

Discussion: Although Dall placed *Nitidiscala catalinae* (Figure 29), in the subgenus *Crisposcala* DURHAM (1937: 483) states, "*Crisposcala* has a basal disk; it is distinguished by a network of crossed spiral lines that produce a decussate appearance on the varices. Living in New Caledonia (De-Boury) Eocene to Recent." As seen in well-preserved specimens, the species is most unusual because of the overlapping costae. Most specimens have suffered damage and are sometimes difficult to identify.

Nitidiscala tabulata (USNM 109569) (Figure 30) the holotype of which has 16 costae, $5\frac{1}{2}$ remaining whorls, is here considered a synonym of *N. catalinae*. The type of *Nitidiscala regum* (USNM 206596) (Figure 31) with 19 costae and 5 remaining whorls is a badly damaged specimen of *N. catalinae*.

Nitidiscala catalinense (Dall, 1917)

(Figure 28)

Epitonium sawinae, variety ? *catalinense* DALL, 1917: 481. STRONG, 1930: 191; pl. 20, fig. 10.

Epitonium (*Nitidoscala*) [sic] *catalinensis*: DALL, 1921: 116. *Epitonium catalinensis*: WILLETT, 1937b: 401. BURCH, 1945: 30. ABBOTT, 1974: 119.

Epitonium catalinense: I. S. OLDROYD, 1927: 61. KEEN, 1937: 35.

Epitonium sawinae catalinense: BOSS, et al., 1968: 68.

Original Description: "Shell with a small three-whorled nucleus, smooth and white, and seven and a half subsequent whorls; varices 22 to 24, not spinose or angular, not regularly continuous over the suture, with the anterior faces of

the varices finely lamellose or deeply striated. Base rounded with a minute umbilical perforation in the adult; aperture nearly circular. Length, 13.5; diameter, 6 mm. Range, off Catalina Island, California. It differs from *sawinae* by the absence of angularity on and the greater number of varices, and by the umbilical perforation." (DALL, 1917: 481).

Additional Description: Shell white, thin, nuclear whorls 3, smooth, amber colored; post nuclear whorls 9 to 10, very inflated, glossy; costae 19 to 30 or more, thin, with a few axial striations on the faces; sutures definite but not deep; base rounded; aperture oval, with reflected face resting on the anterior costae; peritreme complete but very thin and easily broken, barely covering a minute umbilicus. On older specimens, a lime deposit covers all but the upper $\frac{1}{4}$ of each nuclear whorl giving the appearance of a dark, circular band at the top of each whorl. On the fourth whorl down sculpture of fine costae covers half of the whorl, the remainder being amber in color. Length 3 to 22 mm; width .75 to 8 mm.

Type Material and Type Locality:

Epitonium sawinae, variety ? *catalinense* Dall: Holotype, USNM 109502; off Catalina Island, California.

Distribution, Ecology and Bathymetric Range: Vancouver Island, British Columbia ($50^{\circ}40'05''$ N, $128^{\circ}31'9''$ W), south to Todos Santos Island, Baja California Norte ($31^{\circ}53'20''$ N, $116^{\circ}48'15''$ W). Occurs in mud, gray-green sand or gravel substrate in from 20 to 360 m depths.

Geologic Record: Pliocene to Recent.

Upper Pliocene: San Diego Formation, southwestern-most San Diego County, LACMIP locs. 305 [82], 318 [9], and 319 [4].

Lower Pleistocene: Lomita Marl, in San Pedro, at old Hilltop Quarry, LACMIP loc. 64 [1], and below Park Western Drive and Host Place, LACMIP loc. 435 [13].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP loc. 59 [2] (WILLETT, 1937b: 401).

Recent Records: NW tip of Vancouver Island, British Columbia ($50^{\circ}40'5''$ N, $128^{\circ}31'9''$ W), dredged by D. B. Quayle on *A. P. Knight*, FRB Station 68-10, 110 m, 1968, two specimens (LACM 68-177). Pacific Grove, Monterey Bay, California, collected by McLean, in 36 m, 1960, two specimens (LACM 60-23). Southwest side of Santa Rosa Island, Santa Barbara County, California, dredged by *Velero III*, 1941, 77-81 m, on green mud, one specimen (LACM-AHF 1390-41). East side of Santa Barbara Island, California, collected McLean and Margetts, diving at 30 to 70 feet, 1972, one specimen (LACM 72-97). Four miles

north of Todos Santos Island, Baja California Norte, Mexico, dredged by *Velero III*, 1941, in 74 m, from shell, mud, gray sand substrate, one specimen (LACM-AHF 1245-41).

Discussion: Although named as a variety of *Nitidiscala sawinae* by DALL (1917: 481), *Nitidiscala catalinense* is distinct (Figure 28). It differs by having a more tabulate outline, with more inflated (convex) whorls, a deeper suture, more costae, and a minute umbilicus partially hidden by the thin, reflected lip. This species is not rare but is usually encountered in from 20 to 360 m off the islands of the Santa Barbara Channel group. WILLETT (in BURCH 1945: 30) states, "Specimens taken in 20-40 fms [36 to 72 m], (San Pedro, Catalina), vary greatly, some shoulders being rounded, others angled and varices numbering from 19-27 . . . However, 12 specimens taken at 200 fms [360 m] off Catalina Island all have shoulders rounded and varices are more in number, 25 to 32."

Nitidiscala hindsii (Carpenter, 1856)

(Figures 32 to 35)

[For a complete synonymy on this species in the southern part of its range (Panamic Province), see DUSHANE (1974: 34)].

Scalaria hindsii CARPENTER, 1856: 165. CARPENTER, 1857a: 284, 336.

Scala hindsii: ARNOLD, 1903: 264.

Epitonium (Nitidiscala) hindsii: PALMER, 1963: 331; plt. 67, figs. 3-6. DUSHANE, 1974: 15, 34-35; figs. 79-81, 83-84, 87-88.

Not *Epitonium* or *Scalaria hindsii* of California authors (e.g., KEEP, 1911: 183, fig. 174 = *E. tinctum* (Carpenter) q. v.

Epitonium (Nitidoscala) [sic] fallaciosum DALL, 1917: 478 (*nomen nudum*). WOODRING, 1931: 31. BOSS, *et al.*, 1968: 126 ("new name"). [Invalid, lacking indication.]

Not *E. (N.) fallaciosum* DALL, 1921 = *E. tinctum* (Carpenter), q. v.

Epitonium persuturum DALL, 1917: 478. OLDROYD, 1927: 59.

Epitonium (Nitidoscala) [sic] persutura: DALL, 1921: 115.

Epitonium (Nitidiscala) contrerasi JORDAN & HERTLEIN, 1926: 446; plt. 30, fig. 4. GRANT & GALE, 1931: 858. DURHAM, 1937: 488.

Epitonium (Nitidiscala) cooperi STRONG, 1930: 194; plt. 20, figs. 6-8. WILSON & KENNEDY, 1967: 251.

Epitonium (Epitonium) cooperi: ABBOTT, 1974: 119; fig. 1236.

Original Description of *Nitidiscala hindsii* (Carpenter): "S. testa 'S. Cumingii' simili, sed magis elongata, majore, anfr. x. haud profunde separatis; varicibus acutis viii., acutis coronatis, lineis regularibus, ad marginem alteram spirae

parallelis, ascendentibus. Long. 1.04, long. spir. .79, lat. .4, div. 25°." (CARPENTER, 1856: 165).

Additional Description: Shell medium to large in size, white, nuclear whorls three; opaque, postnuclear whorls seven to eleven, loosely coiled; costae eight to fourteen, sharp, high, thin, with an angle or sharp spine at the shoulder, free of the reflected outer lip; suture deep and at an angle, giving the whorls a slanted appearance; aperture oval; operculum horny, thin, paucispiral. Length 3 to 26 mm; width 1½ to 10 mm.

Type Material and Type Localities:

Scalaria hindsi Carpenter: Syntypes (2), BM(NH) 1963.21; Panama. Lectotype designated herein, BM(NH) No. 1963.21, larger of the two syntypes (length 25 mm; width 10 mm).

Epitonium fallaciosum Dall: California (no locality; figured specimen of Keep, present repository undetermined).

Epitonium persuturum Dall: Holotype USNM 211021; San Diego, California.

Epitonium (Nitidiscala) contrerasi Jordan and Hertlein: Holotype CAS (GTC) 2121: Turtle Bay, Baja California Sur, Mexico; CAS loc. 945, Pliocene.

Epitonium (Nitidiscala) cooperi Strong: Holotype SDNHM 345; paratypes SDNHM 3386-3391; USNM 46222, and 56052; San Pedro, California.

Distribution, Ecology and Bathymetric Range: From Forrester Island, Alaska (54°50'N, 133°32'W), south along the north temperate coast including the outer coast of Baja California, the Gulf of California, and south to Peru (14°

14°08'S, 76°08'30"W). Intertidal to 195 m, on mud, silty sand, or gravel bottoms.

Geologic Record: Pliocene to Recent.

Upper Pliocene: Fernando Formation, downtown Los Angeles, Fifth and Hope Streets, LACMIP loc. 27 [1, 4 f.], and Sixth and Hope Streets, LACMIP loc. 466 [6]. San Diego Formation, southwesternmost San Diego County, LACMIP loc. 305 [12]. Turtle Bay, Baja California Sur, Mexico, CAS loc. 945 (Jordan and Hertlein, 1926: as *E. contrerasi*).

Lower Pleistocene: Santa Barbara Formation, east of Santa Barbara General Hospital, LACMIP loc. 183-A [1].

Upper Pleistocene: Isla Vista, near Goleta, LACMIP loc. 416 [2]. Palos Verdes Sand, Lincoln Avenue, near Playa del Rey (Los Angeles), LACMIP locs. 59 [11], and 4745 [103], near Vermont Avenue and Sepulveda Boulevard, west of Carson, LACMIP loc. 147 [3], south of Union Oil Refinery, northern San Pedro, LACMIP loc. 1210 [25]. Formation uncertain, in San Pedro, at San Pedro and Wilmington Road, LACMIP loc. 299 [7], Second and Orizaba [now Beacon] Streets, LACMIP loc. 142 [7], below old Nob Hill, LACMIP loc. 300 [18], and at Arnold's lumberyard exposure, LACMIP loc. 76 [4]. West of Interstate 405 and Cherry Avenue, Long Beach, LACMIP loc. 424 [3]. East bluff above Newport Bay, Newport Beach, LACMIP locs. 66-2 [141] (KANAKOFF & EMERSON, 1959: 27 as *N. indianorum*, in part), 66-1 [7], 66-9 [1],

Explanation of Figures 36 to 48

Figure 36: *Epitonium (Nitidiscala) indianorum* (Carpenter, 1865). Lectotype of STRONG (1930: plt. 20, fig. 1) USNM 15521, "Neeah Bay - J. G. Swan;" length, 26 mm; width, 9 mm
× 1.88

Figure 37: *Epitonium columbianum* Dall, 1917. Holotype, USNM 111211; length, 21 mm; width, 7.5 mm
× 2.1

Figure 38: *Epitonium montereyense* Dall, 1917. Holotype, USNM 111217; length, 6 mm; width, 2.5 mm
× 4.8

Figure 39: *Scala rectilaminata* Dall, 1907. Holotype, USNM 110430; length, 3.25 mm; width, 1.6 mm
× 2

Figure 40: *Scala berryi* Dall, 1907. Holotype, USNM 107724; length, 3.5 mm; width, 1.75 mm
× 2

Figure 41: *Nitidiscala tinctoria* (Carpenter, 1865). Laguna de San José, Baja California Norte, Mexico, specimens with egg clusters, in tide pools with large sea anemones (DuShane Collection)

Figure 42: *Nitidiscala sawinae* (Dall, 1903). Santa Barbara Island, California; length, 19 mm; width, 7 mm (DuShane Collection)
× 2.5

Figure 43: *Epitonium (Crisposcala) acrostephanus* Dall, 1908. Holotype, USNM 110638; length, 20 mm; width, 6.5 mm
× 7

Figure 44: *Scala sawinae* Dall, 1903. Holotype, USNM 109309; length, 10.5 mm; width, 4 mm
× 7.5

Figure 45: *Scalaria subcoronata* Carpenter, 1866. Holotype, USNM 14830b; length, 13 mm; width, 7 mm
× 3.8

Figure 46: *Epitonium tinctum* var. *bormanni* Strong, 1941. Paratype, DuShane Collection; length, 4.5 mm; width, 2.5 mm
× 11.7

Figure 47: *Epitonium continuatum* T. S. Oldroyd, 1925. Holotype, USNM 352383 (type lost since 1952, *vide* Rosewater, 1975); length, 8 mm; width, 3.6 mm. Figure from T. S. Oldroyd (1925: plt. 2, fig. 10)
× 6.5

Figure 48: *Scalaria* (? *Indianorum*, var.) *tinctoria* Carpenter, 1865. Lectotype of PALMER, (1958: 189); USNM 19510; length, 10.5 mm; width, 4.5 mm
× 4.5



Figure 36

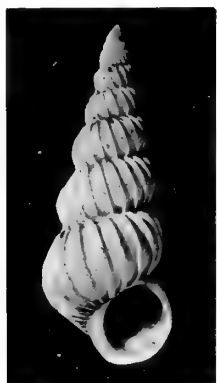


Figure 37



Figure 38



Figure 39



Figure 40



Figure 41



Figure 42



Figure 43



Figure 44



Figure 45



Figure 46



10

Figure 47



Figure 48

and 136 [43]. Pacific Coast Highway, below Newport Heights, Newport Beach, LACMIP loc. 241 [1]. Near MacArthur Boulevard and San Joaquin Hills Road, Newport Beach, LACMIP loc. 480 [1]. Bay Point Formation, old Spanish Bight, Coronado Island (San Diego), LACMIP loc. 336 [2], and on Pomona Street, Glorietta Bay, Coronado, LACMIP loc. 2658 [1].

Recent Records: *Nitidiscala hindsii* ranges from Forrester Island, Alaska ($54^{\circ}50'N$, $133^{\circ}32'W$), south to Independencia Bay, Peru ($14^{\circ}14'08''S$, $76^{\circ}08'30''W$), with documentation of many stations throughout its range. Forrester Island, Alaska, *ex* Antoniss Jay Collection [53 specimens, dead. Intertidal ?] (LACM 13448). Venado Island, Canal Zone, Panama, collected McLean, 1970, one specimen (LACM 70-15). Independencia Bay, Peru, *Velero* III, 1935, two specimens (LACM-AHF 380-35).

Discussion: CARPENTER (1856: 165) described *Scalardia hindsii* from Panama. He later recognized the species in the California fauna, but because some of the material so identified turned out to be *Epitonium tinctum*, there has been confusion. Dall attempted to recognize the California form as distinct, but unfortunately in proposing the name *E. fallaciosum* for it in 1917 he gave no real diagnosis, cited no type specimen, and did not select a type locality. In 1921 he remedied the oversight by citing a figure, based on KEEN (1911: 183, fig. 174), but unfortunately one that authors agree is of *E. tinctum*. Because there is a geographically consistent pattern of variation within *Nitidiscala hindsii*, it would be convenient to recognize two geographic subspecies (drawing the boundary line between them, however, might be difficult)—the southern or Panamic subspecies having a larger shell, with fewer costae (8 to 9) the northern variant tending to be smaller with up to 14 costae. The name for the latter, given by Strong, *Epitonium cooperi*, has been accepted by many authors as taking the place intended by Dall for his *E. fallaciosum*. WOODRING's attempt (1931) to supply an "indication" for the latter by designating a "lectotype" was futile, for Dall had in 1921 supplied the indication when he cited a figure, though that turns out to represent another species. Against adoption of *E. cooperi* stands the barrier of two prior synonyms: *E. persuturum* Dall, 1917, based on a beachworm shell, and *E. contrerasi* Jordan and Hertlein, 1926, based on a fossil. Neither has received much currency. Because of this matter of priority, it seems better to regard the shift in morphological characters from south to north as clinal and to consider that the true range of *N. hindsii* is from Alaska to Panama.

DUSHANE (1974: 34-35) synonymized 6 nominal species from the Panamic-Galapagan region with *Nitidiscala hind-*

sii. In addition, *Epitonium persuturum* Dall, and *Epitonium cooperi* Strong are synonymized herein.

According to BURCH (1945: 29), *Nitidiscala hindsii* is commonly dredged off the southern California coast in from 65 to 195 m, on a gravel substrate. It is often washed in by the hundreds on beaches after a storm. Common as dead shells are, I have seen only one live-taken specimen, dredged in 11 to 15 m off Puertecitos, Gulf of California, Mexico, December, 1964 (DuShane Collection).

Nitidiscala indianorum (Carpenter, 1865)

(Figures 36, 37, 38)

- Scalardia indianorum* CARPENTER, 1864: 613, 628, 660, 683 [reprinted, 1872: 99, 114, 146, 149]. CARPENTER, 1865: 10 [Reprinted, 1872: 244]. COOPER, 1888: 263. SOWERBY, in REEVE, 1873: pl. 11, fig. 81. DALL, 1878a: 27, 28. DALL, 1878b: 12. ORCUTT, 1885: 539. TRYON, 1887: 70; pl. 14, figs. 48, 49.
- Scala indianorum*: ARNOLD, 1903: 15, 19, 22, 24, 25, 28, 31, 45, 264. ARNOLD, 1906: 31, 36.
- Epitonium indianorum*: KEEP, 1911: 183. MOODY, 1916: 43. T. S. OLDROYD, 1925: 13. I. S. OLDROYD, 1927: 57, 58. KEEN, 1937: 35. KEEN, 1943: 37. WILLETT, 1937b: 32. MORRIS, 1952: 87; pl. 24, fig. 4. EMERSON & ADDICOTT, 1953: 439. VALENTINE, 1961: 360. ADDICOTT & EMERSON, 1959: 15, 21. KANAKOFF & EMERSON, 1959: 27. VALENTINE & MEADE, 1961: 12, 17, 23. ADDICOTT, 1966: 4; pl. 2, fig. 29. BERNARD, 1970: 81. ABBOTT, 1974: 119.
- Epitonium (Nitidoscala) [sic] indianorum*: DALL, 1917: 477. DALL, 1921: 115. I. S. OLDROYD, 1924: 107. I. S. OLDROYD, 1927: 57. STRONG, 1930: 186, 192; pl. 20, figs. 1, 2a-b. GRANT & GALE, 1931: 859.
- Epitonium (Nitidiscala) indianorum*: T. S. OLDROYD, 1925: 13. DURHAM, 1937: 481, 487; pl. 56, fig. 14. WILLETT, 1937b: 401. KEEN & BENTSON, 1944: 155. BURCH, 1945: 24, 27. A. G. SMITH & GORDON, 1948: 191. BERRY, 1956: 153. PALMER, 1958: 186; pl. 20, figs. 23, 24. GLEN, 1959: 185; fig. 5. WILSON & KENNEDY, 1967: 252. MOORE, 1968: 58; pl. 27, fig. g.
- Epitonium (Gyroscale) indianorum*: ABBOTT, 1974: 165.
- Epitonium columbianum* DALL, 1917: 481. I. S. OLDROYD, 1927: 60. KEEN, 1937: 35. BURCH, 1945: 30. BOSS *et al.*, 1968: 85.
- Epitonium (Nitidoscala) [sic] columbiana*: DALL, 1921: 115.
- Epitonium (Epitonium) indianorum*: ABBOTT, 1974: 122.
- Epitonium montereyense* DALL, 1917: 481 [not *Scala (Cirso-trema) montereyensis* DALL, 1907]. I. S. OLDROYD, 1927: 57. BOSS, *et al.*, 1968: 213.
- Scalardia regiomontana* DALL in DEBOURY, 1919: 39 (new name for *E. montereyense* Dall, 1917).
- Scalardia (Nitidoscala) [sic] regiomontana* 'Dall, 1917' [sic]: DALL, 1921: 116 [new name for *montereyense* Dall, 1917]. BOSS, *et al.*, 1968: 275.
- Epitonium regiomontanum*: I. S. OLDROYD, 1927: 64. KEEN, 1937: 35. BURCH, 1945: 31. SMITH & GORDON, 1948: 191.

Epitonium (Epitonium) regiomontanum: ABBOTT, 1974: 122.

Original Description of *Nitidiscala indianorum* (CARPENTER, 1865): "Scalaria testa gracili, turrata, alba: anfr. circ. X., rotundatis, parum separatis, laevibus; basi simplici, haud umbilicata; costis viii.-xv. (plerumque xii), acutioribus, subreflexis, interdum latis, plerumque lineis irregularibus margini spirae recto parallelis ascendentibus, rarius juxta suturam subnodosis; apertura ovata. Long. 1.05, long. spir. .8, lat. .36, div. 28. Hab. Neeah Bay (Swan). Strung as ornaments by the Indian children. Intermediate between *S. communis* and *S. Turtonis*, and scarcely differs from '*S. Georgettina*, Kien.,' Mus. Cum. No. 34, Brazil." (CARPENTER, 1865: 10).

Additional Description: Shell large in size, white, solid; whorls 8 to 10, convex, with longitudinal growth lines; costae 10 to 17, low, rounded, somewhat striated, continuous over the suture which is shallow; at the suture each costa joining the one above and extending along the suture to the next costa on the left; costae on the lower and middle portion somewhat reflected unless worn, when they appear to be thick, rarely with a small spine at the shoulder; costae continuous to the base and the columellar lip, to which they fuse; non-umbilicate, lip entire; operculum horny, paucispiral. Length 7.4 to 38 mm; width 3.3 to 12 mm.

Type Material and Type Localities:

Scalaria indianorum Carpenter: Lectotype USNM 15521 by STRONG (1930: pl. 20, fig. 1); paralectotypes (4) plus fragments (2) USNM 635564; Neah Bay, Washington.

Epitonium (Nitidoscala) [sic] columbianum Dall: Holotype USNM 111211; off the Columbia River, Oregon.

Epitonium montereyense Dall: Holotype USNM 111217 (rejected homonym of *Scala (Cirsotrema) montereyensis* Dall, 1907); Monterey Bay, California.

Distribution, Ecology and Bathymetric Range: Forrester Island, Alaska ($54^{\circ}50'N$, $133^{\circ}32'W$), south to Todos Santos Bay, Baja California Norte, Mexico ($31^{\circ}53'N$, $116^{\circ}48'W$); intertidal to 114 m; sandy mud substrate.

Geologic Record: ? Miocene, Pliocene to Recent.

Upper Pliocene: Fernando Formation, near Interstate 405 and Cherry Avenue, Long Beach, LACMIP loc. 423 [1]. San Diego Formation, southwesternmost San Diego County, LACMIP loc. 305-C [1].

Lower Pleistocene: Port Orford Formation, southeast of Cape Blanco and north of old mouth of Elk River, Oregon, LACMIP locs. 3947 [12, 3 f.], 3949 [1], and 3960 [7]. Elk Head, north of Trinidad, LACMIP loc. 3941 [1]. Crannell Road and highway 101 frontage road, south of Trinidad, LACMIP loc. 3936 [19]. Santa Barbara Formation, Rincon Hill Road, southeast of Carpinteria, LACMIP loc. 473 [1]. Stockton Ranch,

Las Posas Hills (Ventura County), LACMIP loc. 161 [3]. Don Felipe Drive, Baldwin Hills, Los Angeles, LACMIP loc. 293 [1]. Lomita Marl, in San Pedro, at old Hilltop Quarry, LACMIP loc. 64 [9], and below Host Place and Park Western Drive, LACMIP loc. 435 [21].

Upper Pleistocene: Near Cayucos, LACMIP loc. 421 [5]. Isla Vista, near Goleta, LACMIP loc. 2694 [1]. San Pedro Sand, Second and Orizaba [now Beacon] Streets, San Pedro, LACMIP loc. 142-B [5]. Formation uncertain, in San Pedro, at Pacific Avenue and Oliver Street, LACMIP loc. 131 [1], Third and Mesa Streets, LACMIP loc. 98 [3], and at Deadman Island, LACMIP loc. 2 [4, 1 f.]. Palos Verdes Sand, Lincoln Avenue, Playa del Rey (Los Angeles), LACMIP locs. 59 [29] (Willett, 1937b: 401), and 4745 [14], Anaheim Street, east of Normandie Avenue, Harbor City (Los Angeles), LACMIP loc. 229 [6], San Pedro, LACMIP loc. 2695 [1 f.], Eighth and Palos Verdes Streets, San Pedro, LACMIP loc. 226 [3], "Crawfish Georges," 22nd and Mesa Streets, San Pedro, LACMIP loc. 2697 [2], Pacific Coast Highway between Seventh and Colorado Streets, Long Beach, LACMIP loc. 4568 [4] (KENNEDY, 1975: 30; as cf.). East bluffs above Upper Newport Bay, Newport Beach, LACMIP loc. 66-2 [1] (KANAKOFF & EMERSON, 1959: 27; in part). Pacific Coast Highway, below Newport Heights, Newport Beach, LACMIP loc. 241 [1].

Recent Records: Forrester Island, Alaska, collected by Willett (1914-1917), 72 m (USNM 216346). Neah Bay, Washington, collected by J. G. Swan, five specimens and fragments (USNM 15521 and 635564). Off the Columbia River, Oregon, taken by the U.S. Fish Commission, station 3065, 49 m, fine black sand, length 21 mm; width 7.5 mm, with nine whorls and 17 costae as *Epitonium columbianum* Dall, 1917 (USNM 111211), Monterey Bay, Monterey County, California, taken by the U. S. Fish Commission, station 4140, in 54 m, length 6 mm; width 2.5 mm; with 6 whorls and 14 costae as *Scalaria regiomontana* Dall, 1921 (USNM 111217), Carmel Submarine Canyon, Monterey County, California, collected by McLean diving at 40 to 125 feet, one live-taken specimen, length 38 mm; width 7 mm, with 12 whorls and 13 costae (LACMIP 60-24). Todos Santos Bay, Baja California Norte, Mexico, taken by the U.S. Fish Commission, station 2936, in 108 m, juvenile specimens (USNM 209427).

Discussion: The range of *Nitidiscala indianorum* is extensive along the coast from Alaska south to Todos Santos Bay, Baja California Norte, Mexico. Southern specimens

are smaller, indicating the terminus of the range. Two nominal species, *Nitidiscala columbiana* and *Nitidiscala regiomontana* are placed in synonymy herein because no differences in shell characters can be found. Each is within the geographical range for *N. indianorum*. DALL (1917: 481) based his southern record of *N. columbiana* (USNM 97027) dredged off Punta Abreojos, Baja California Sur, Mexico on 1 specimen that appears to be of another species.

Nitidiscala indianorum is sometimes confused with *N. tinctoria*, but has a much larger shell and lacks the brown sutural line sometimes found in *N. tinctoria*. *Nitidiscala indianorum* also occupies a more northern, although somewhat overlapping, geographical range. It is also found only sublittorally and must be dredged or obtained by diving, whereas *N. tinctoria* occurs mainly intertidally.

Although Carpenter mentioned *Nitidiscala indianorum* several times in 1864, he did not describe the species until 1865, indicating that it was intermediate between *Scalaria communis* and *S. turtonis*.

When PALMER (1958: 187; pl. 20, figs. 23, 24) chose a syntypic specimen of *Nitidiscala indianorum* as lectotype and a second specimen as a paratype she was unaware that STRONG (1930: pl. 20, fig. 1) had already chosen a lectotype (USNM 15521) (length 26 mm; width 9 mm), which had probably been segregated from the other syntypic specimens. All remaining specimens (USNM 635564), other than the lectotype chosen by Strong, became paralectotypes.

Nitidiscala sawinae (Dall, 1903)

(Figures 39, 40, 42, 43, 44)

- Scala sawinae* DALL, 1903: 175. KELSEY, 1907: 49. DALL & BARTSCH, 1910: 21. BOSS, *et al.*, 1968: 287.
- Epitonium sawinae*: DALL, 1907: 481. PACKARD, 1918: 319; pl. 36, fig. 13. STRONG, 1930: 191, 194; pl. 20, figs. 9, 10. KEEN, 1937: 35. WILLETT, 1937a: 64. BURCH, 1945: 30. ABBOTT, 1974: 119; fig. 1237. DUSHANE, 1974: 39.
- Epitonium (Nitidoscala) [sic] sawinae*: DALL, 1921: 115; pl. 6, fig. 12.
- Epitonium (Nitidoscala) sawinae*: STRONG, 1945: 24, 27. SMITH & GORDON, 1948: 191.
- Scala berryi* DALL, 1907: 127. BERRY, 1907: 42. BOSS, *et al.*, 1968: 46.
- Epitonium berryi*: DALL, 1917: 483. KEEN, 1937: 35. STRONG, 1945: 27. BURCH, 1945: 31, 32.
- Epitonium (Nitidoscala) [sic] berryi*: DALL, 1921: 116. I. S. OLDROYD, 1927: 63.
- Epitonium (Nitidoscala) berryi*: STRONG, 1945: 25. SMITH & GORDON, 1948: 190.
- Epitonium (Epitonium) berryi*: ABBOTT, 1974: 123.
- Scala rectilaminata* DALL, 1907: 127. BERRY, 1907: 42. BOSS, *et al.*, 1968: 274.
- Epitonium rectilaminatum* DALL, 1917: 482 (*lapsus* for *Scala*

rectilaminata DALL, 1907: 127). I. S. OLDROYD, 1927: 62. KEEN, 1937: 35. STRONG, 1945: 27. BURCH, 1945: 31, 32. SMITH & GORDON, 1948: 191. KANAKOFF & EMERSON, 1959: 27.

Epitonium (Epitonium) rectilaminatum: ABBOTT, 1974: 122.

Epitonium (Crisposcala) acrostephanus DALL, 1908: 251. BURCH, 1945: 32. BOSS, *et al.*, 1968: 9.

Epitonium acrostephanus: DALL, 1917: 478. KEEN, 1937: 35. VALENTINE & MEADE, 1961: 23. COWAN, 1964: 111.

Epitonium (Nitidoscala) [sic] acrostephanus: DALL, 1921: 116.

Epitonium (Nitidoscala) [sic] acrostephanus: T. S. OLDROYD, 1925: 13. I. S. OLDROYD, 1927: 65.

Epitonium acrostephanus: KANAKOFF & EMERSON, 1959: 27.

Epitonium (Nitidoscala) acrostephanus: GRANT & GALE, 1931: 858. WILLETT, 1937b: 401.

Epitonium (Crisposcala) acrostephanus: SMITH & GORDON, 1948: 191.

Epitonium (Epitonium) acrostephanus: ABBOTT, 1974: 123.

Original Description of *Nitidiscala sawinae* (DALL, 1903): "Shell small, elongate, sub-acute, with ten or more whorls; nucleus of three smooth polished whorls; subsequent whorls smooth, with about 19 low, sharp, slightly reflected varices which entirely cross the whorl; at the shoulder these are slightly spinose; aperture rounded ovate, entire, with a small spine at the shoulder angle and a less conspicuous one at the inner base of the aperture; there is no trace of a basal cord or disk, and no spiral sculpture. Length, 10.5; diameter of aperture, 2.5; max. diameter of last whorl 4.0 mm. A broken specimen with three more whorls seems to have measured 24 mm in total length when perfect, and 8 mm in diameter." (DALL, 1903: 175).

Additional Description: Shell medium to large; white; nuclear whorls 2 to 3, usually broken, sometimes with a small, round plug formed inside the last nuclear whorl; remaining whorls 8 to 10, smooth, with occasional fine axial striations; suture deep; costae 14 to 21, reflected, with a sharp spine at the shoulder, slightly striate longitudinally, with a turn into the suture, crossing it and becoming connected with one of the costae of the preceding whorl, slightly flattened at the base; aperture ovate; peritreme thin, reflected over the costae on which they rest; non-umbilicate; operculum thin, horny, paucispiral, horn color. Length 3.5 to 24 mm; width 1 to 8 mm.

Type Material and Type Localities:

Scala sawinae Dall: Holotype USNM 109309; Avalon, Catalina Island, California.

Scala berryi Dall: Holotype USNM 107724; San Pedro Bay, California.

Scala rectilaminata Dall: Holotype USNM 110430; Monterey Bay, California.

Epitonium (Crisposcala) acrostephanus Dall: Holotype USNM 110638. Newport, California.

Distribution, Ecology and Bathymetric Range: British Columbia, Canada ($54^{\circ}17'N$, $132^{\circ}37'W$), south to Magdalena Bay, Baja California Sur, Mexico ($24^{\circ}31'30''N$, $112^{\circ}01'10''W$). Occasionally taken by divers, but usually dredged in mud, sand and broken shell substrate in from 18 to 360 m.

Geologic Record: Pliocene to Recent.

Upper Pliocene: Fernando Formation, downtown Los Angeles, at Fifth and Hope Streets, LACMIP loc. 19 [2], and at Sixth and Hope Streets, LACMIP loc. 466 [18]. San Diego Formation, Pacific Beach, LACMIP loc. 309 [1], Market Street, San Diego, LACMIP loc. 127 [1], southwesternmost San Diego County, LACMIP locs. 305 [109], 305-A [158], 305-C [18], 318 [4], and 319 [5].

Lower Pleistocene: Port Orford and Elk River Formations, southeast of Cape Blanco and north of old mouth of Elk River, Oregon, LACMIP locs. 3947 [7] and 3960, Moonstone Beach, south of Trinidad, LACMIP loc. 3942 [13, 4 f.], Santa Barbara Formation, east of Santa Barbara General Hospital, LACMIP locs. 183-A [15], and 183-B [22], Santa Barbara County Dump, LACMIP loc. 322 [4, 1 f.], bluff on Santa Barbara Yacht Harbor, LACMIP loc. 4965 [1], Rincon Hill Road, southeast of Carpinteria, LACMIP loc. 4890 [6]. Ondulando Highlands, Ventura, LACMIP loc. 441 [4]. Lomita Marl, in San Pedro, at old Hilltop Quarry, LACMIP loc. 64 [5], and below Host Place and Park Western Drive, LACMIP loc. 435 [130]. Timms Point Silt, Timms Point, San Pedro, LACMIP locs. 62 [9], and 130-7 [12].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP locs. 59 [105] (WILLETT, 1937b: 401; as *E. (N.) sawinae*

and *E. (N.) acrostephanum*), and 4745 [2], Vermont Avenue and Sepulveda Boulevard, west of Carson, LACMIP loc. 147 [2], and Lomita Boulevard and Main Street, Wilmington (Los Angeles), LACMIP loc. 77 [27]. Terrace seven, Palos Verdes Hills, LACMIP loc. 1308 [2] (MARINGOVICH, 1976: 23; as *E. sp.*). Formation uncertain, in San Pedro, Pacific Avenue and Oliver Street, LACMIP loc. 131 [1], Second and Orizaba [now Beacon] Streets, LACMIP loc. 142 [6], and Deadman Island, LACMIP loc. 2 [1]. Near Interstate 405 and Cherry Avenue, Long Beach, LACMIP loc. 424 [2]. East bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-2 [26] (KANAKOFF & EMERSON, 1959: 27; as *E. rectilaminatum* and *E. acrostephanum*), 66-1 [6], and 136 [4]. West bluff of "middle" Newport Bay, Newport Beach LACMIP locs. 68-A [1] (KANAKOFF & EMERSON, 1959: 27; as *E. rectilaminatum*) and 68-B ["3" specimens missing] (KANAKOFF & EMERSON, 1959: 27; as *E. acrostephanum*).

Recent Records: This species occurs off the Queen Charlotte Islands, British Columbia, along the Oregon and southern California coasts, including the offshore islands of Santa Rosa, Santa Cruz, Catalina, San Martin, Guadalupe, as far south as Magdalena Bay, Baja California Sur, Mexico, in from 18 to 360 m.

Off the northwest tip of Graham Island, Queen Charlotte Islands, British Columbia, Canada, collected by F. Bernard (*G. B. Reed*, station 67-32), 179 m, August 1967, one live but damaged specimen with operculum intact (LACM 67-30). La Perouse Bank, Barkley Sound, Vancouver Island, British Columbia, Canada, dredged by Cowan (1964: 111), one live specimen (no depository given), 72 m. Monterey Bay, California, length 3.5 mm; width 1 mm, 22 m, 1 specimen as

Explanation of Figures 49 to 59

- | | |
|---|--|
| Figure 49: <i>Opalia insculpta</i> Carpenter, 1865. Holotype, PRI 7090 (formerly Cornell Univ. 4950); length, 14 mm; width, 7 mm $\times 4$ | Figure 54: <i>Opalia tremperi</i> Bartsch, 1927. Holotype, USNM 362-454; length, 7.8 mm; width, 2.5 mm $\times 7$ |
| Figure 50: <i>Opalia (Dentiscala) crenimarginata</i> Dall, 1917. Holotype, USNM 111207; length, 17 mm; width, 7 mm $\times 3.7$ | Figure 55: <i>Rissoa infrequens</i> C. B. Adams, 1852. Holotype, MCZ 186418; length, 6.5 mm; width, 2 mm $\times 7.6$ |
| Figure 51: <i>Opalia (Dentiscala) nesiotica</i> Dall, 1917. Holotype, USNM 56900; length, 10.5 mm; width, 5 mm $\times 6$ | Figure 56: <i>Opalia mazatlanica</i> Dall, 1908. Holotype, USNM 168669; length, 12.5 mm; width, 4.5 mm $\times 5$ |
| Figure 52: <i>Scalaria (Cirsotrema) funiculata</i> Carpenter, 1857. Lectotype of KEEN (1968: 408; plt. 57, fig. 50a; text fig. 40) BM(NH); length, 21 mm $\times 2$ | Figure 57: <i>Epitonium (Nodiscala) ordenanum</i> Lowe, 1932. Holotype, ANSP 157988; length, 7 mm; width, 2 mm $\times 7$ |
| Figure 53: <i>Opalia bullata</i> Carpenter, 1865. Holotype, RM No. 76, Montreal, Canada; length, 8 mm; width, 2.5 mm $\times 7$ | Figure 58: <i>Scala (Cirsotrema) [sic] montereyensis</i> Dall, 1907. Holotype, USNM 110431; length, 2.5 mm; width, 1.5 mm $\times 4$ |
| | Figure 59: <i>Scala (Opalia) pluricostata</i> Dall, 1917. Holotype, USNM 56054; length, 16 mm; width, 5 mm $\times 3.1$ |

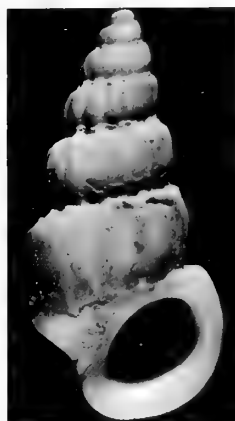


Figure 49



Figure 50



Figure 51



Figure 52

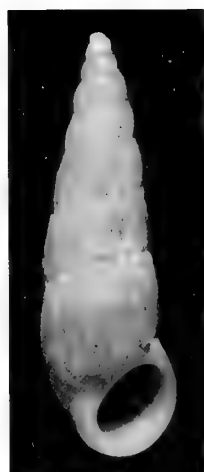


Figure 53

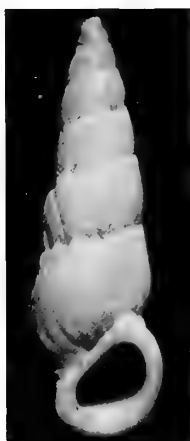


Figure 54



Figure 55



Figure 56



Figure 57

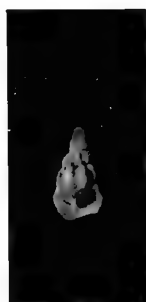


Figure 58

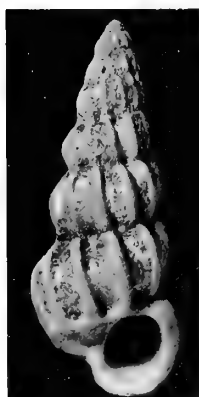


Figure 59

Scala rectilaminata (USNM 110430). Off Naples, California, dredged by Pat Brophy from a kelp holdfast, 290 m, one live specimen, November 1968 (Santa Barbara City College Collection). San Pedro, California, length 3.5 mm; width 1.75 mm, 360 m, one specimen as *Scala berryi* (USNM 107724). The Hancock Expeditions 1931-1941 (*Velero III*) dredged it commonly from Anacapa Island, California south to the Baja California, Mexico outer coast islands of San Martin (station 1694-49), Guadalupe (station 1919-49), Cedros (station 1948-50), and from Magdalena Bay (24°31'30"N, 112°01'10"W).

Discussion: DALL (1903: 175) described *Nitidiscala sawinae* from off Catalina Island, California. The type has a medium sized shell of 10.5 mm and so later workers neglected to assess the relationship to *N. acrostephanus* (DALL, 1908), which is normally 20 mm in length. When the type of *N. sawinae* is photographed and enlarged to a size comparable with *N. acrostephanus* the synonymy is obvious (Figures 43, 44). Both species have the same proportions, 14 to 21 costae, and a similar geographic and depth range. DALL (1908: 251), in his original description, gave the range of this species from Monterey, California to the Coronados Islands, Mexico, in from 29 to 61 m, explaining that the species was common in the dredgings, but was usually smaller than the holotype of *Nitidiscala acrostephanus* dredged by H. N. Lowe off Newport, California. It is odd that STRONG (1922) listed *N. acrostephanus*, but neglected to discuss the species in his (1930) paper on *Nitidiscala* from the west coast of North America.

The characteristics of *Nitidiscala berryi* and *N. rectilaminata*, both of Dall, are essentially the same as those for *N. sawinae* and the 2 are synonymized here (Figures 39, 40). DALL (1917: 483) likened *N. berryi* to *Epitonium inconspicuum* (Sowerby, 1842), from the West Indies, but did not imply synonymy.

In a general statement, DALL (1917: 481) suggested that *Nitidiscala sawinae* ranged into the Gulf of California, Mexico, but did not validate his suggestion with any specific data. There seems to be a species group affinity among a number of nominal species in the genus *Nitidiscala*, namely: *N. curvilineatum* (Sowerby, 1844) from Central America, *N. imbrex* from Panama, *N. willetti* from Mazatlan, Mexico, and *N. sawinae* from California. Unfortunately, the type of *N. curvilineatum* could not be located at the British Museum (Natural History) (*teste* A. M. Keen), so we have only the illustration in SOWERBY (1844: plt. 33, fig. 59) by which to make an evaluation. All the species have many costae, thin, erect, somewhat flattened on the base with a fragile texture and swollen whorls. Perhaps all these taxa may prove to be synonymous with *N. curvilineatum*.

Nitidiscala tincta (Carpenter, 1865)

(Figures 41, 45, 46, 47, 48)

- Scala* ? *Indianorum* var. CARPENTER, 1864a: 613 [Reprinted, 1872: 99].
- Scala* ? var. *tincta*: CARPENTER, 1864a: 660 [Reprinted, 1872: 146].
- Scala* (*Ind. var.*) *tincta*: CARPENTER, 1864a: 665 [Reprinted, 1872: 151].
- Scala* (? *Indianorum*, var.) *tincta*: CARPENTER, 1865: 31 [Reprinted, 1872: 244]. COOPER, 1870: 67.
- Scala tincta*: DALL, 1878b: 12. TRYON, 1887: 70; plt. 14, fig. 49. COOPER, 1888: 263.
- Epitonium* (*Nitidoscala*) [*sic*] *tinctum*: DALL, 1917: 477. T. S. OLDROYD, 1925: 13. I. S. OLDROYD, 1927: 58.
- Scala tincta*: ARNOLD, 1903: 265; plt. 5, fig. 3. ARNOLD, 1906: 28, 36. DEBOURY, 1919: 34.
- Epitonium tinctum*: T. S. OLDROYD, 1925: 13. STRONG, 1930: 190. KEEP, 1935: 180; fig. 153. KEEN, 1937: 36. WILLETT, 1937b: 401. STRONG, 1941: 46. BURCH, 1945: 27, 28. STRONG, 1945: 26. MORRIS, 1952: 88; plt. 24, fig. 5. A. CLARK, 1957: plt. 2. THORSON, 1957: 55. PALMER, 1958: 188. VALENTINE, 1961: 360, 374. VALENTINE & MEADE, 1961: 10, 16. MCLEAN, 1969: 34; fig. 17.1. BERNARD, 1970: 81. HOCHBERG, 1971: 22, 23. C. R. SMITH, 1972: 47. ABBOTT, 1974: 119; fig. 1234. KENNEDY, 1975: 27. R. I. SMITH & CARLTON, 1975: 488. VEDDER & MOORE, 1976: 130; plt. 2, figs. 4, 5. C. R. SMITH, 1977a: 331-340; figs. 1-4. C. R. SMITH, 1977b: 9. MCLEAN, 1978: 34; fig. 17.1.
- Epitonium* (*Nitidoscala*) *tinctum*: STRONG, 1930: 193; plt. 20, figs. 3, 4, 5a-5b. GRANT & GALE, 1931: 859, 860. DURHAM, 1937: 488. WILLETT, 1937b: 401. A. G. SMITH & GORDON, 1948: 191. PALMER, 1958: 188. WILSON & KENNEDY, 1967: 252.
- Epitonium* (*Nitidoscala*) *tincta*: STRONG, 1945: 24.
- Epitonium tinctum* [*sic*]: KANAKOFF & EMERSON, 1959: 27.
- Scala subcoronata* CARPENTER, 1864a: 613, 660 [Reprinted, 1872: 99, 146]. CARPENTER, 1866: 221. COOPER, 1870: 67. DALL, 1874: 297. DALL, 1878b: 29. COOPER, 1888: 263. DEBOURY, 1919 (as *Scala*): 34. STRONG, 1930: 187, 192. PALMER, 1958: 188.
- Epitonium* (*Nitidoscala*) [*sic*] *subcoronatum*: DALL, 1917: 478. I. S. OLDROYD, 1924: 107. I. S. OLDROYD, 1927: 58.
- Epitonium* (*Nitidoscala*) [*sic*] *subcoronata*: DALL, 1921: 115.
- Epitonium subcoronatum*: T. S. OLDROYD, 1925: 13. KEEN, 1937: 35. BURCH, 1945: 28. ABBOTT, 1974: 119 (as a synonym of *E. tinctum*).
- Epitonium continuatum* T. S. OLDROYD, 1925: 13, 35; plt. 2, fig. 10.
- Epitonium* (*Nitidoscala*) *continuatum*: GRANT & GALE, 1931: 858.
- Epitonium* (*Nitidoscala*) *eelense* DURHAM, 1937: 488; plt. 56, fig. 7.
- Epitonium* (*Nitidoscala*) [*sic*] *tinctum* var. *bormanni* STRONG, 1941: 47. BURCH, 1945: 28. WILSON & KENNEDY, 1967: 252.
- Epitonium bormanni*: ABBOTT, 1974: 119, as a "form" of *E. tinctum*.

Original Description of *Nitidiscala tincta* (CARPENTER, 1865): "*S. ? Indianorum* costis acutis, haud reflexis; anfractibus postice fuscopurpureo tinctis. Hab. Cerros Island (Ayres); San Pedro (Cooper).

The Lower-Californian shell may prove distinct. It is like *S. regularis* Cpr., but without the spiral sculpture." (CARPENTER, 1865: 31).

Additional Description: Shell small to medium in size; nuclear whorls 3, rapidly increasing, opaque, solid looking; remaining whorls 4 to 8, sometimes showing a brown area at the sutures, rounded; costae 11 to 14, very slightly reflected, and slightly shouldered on the whorls at times, reflected under the face of the aperture; suture deep; aperture oval, patulous anteriorly, operculum thin, horny, light in color. Length 4 to 15 mm; width 1 to 5 mm.

Type Material and Type Localities:

Scalaria (? *Indianorum*, var.) *tincta* Carpenter: Lectotype USNM 19510 by Palmer (1958: 189) (figured by Strong, 1930: pl. 20, fig. 3); San Pedro, California (collected by Cooper).

Scalaria subcoronata Carpenter: Holotype USNM 14830b; Monterey, California.

Epitonium continuatum T. S. OLDROYD: Holotype USNM 352383 (type lost since 1952; *vide* Rosewater, 1975); Nob Hill Cut, San Pedro, California; Pleistocene (San Pedro Sand).

Epitonium (*Nitidiscala*) *eelense* Durham: Holotype UCMF 30147; Eel River, Humboldt County, California; Pliocene.

Epitonium tinctum var. *bormanni* Strong: Holotype LACM 1064; paratypes (4) SBMNH 08119; paratypes (8) SDNHM 454, 1521-1527; paratypes (13) DuShane Collection.

Distribution, Ecology and Bathymetric Range: Forrester Island, Alaska (54°50' N, 133°32' W), south to Magdalena Bay, Baja California Sur, Mexico (24°18' N, 112°12' W). *Nitidiscala tincta* is a micropredator and occurs intertidally on the small colonial anemone *Anthopleura elegantissima* and less commonly on the large, solitary anemone *Anthopleura xanthogrammica*. The most common habitats are in sand pockets and on open-faced boulders, in sand filled crevices, under kelp, and on rock ledges, from a zero tide down to 40 m. It is capable of withstanding long periods of exposure between tides. During low tide *N. tincta* can be found clustered on the column of the sea anemone cup (the oral disk), but twice each day at high tide it feeds by snipping off the ends of the tentacles of the anemone. Dentition of the radula is in the form of long, bifid structures, unlike any other epitoniid thus far reported. The largest teeth have a long, smooth blade without projections,

while the smaller teeth almost always show projections in this area (Figures 70, 71).

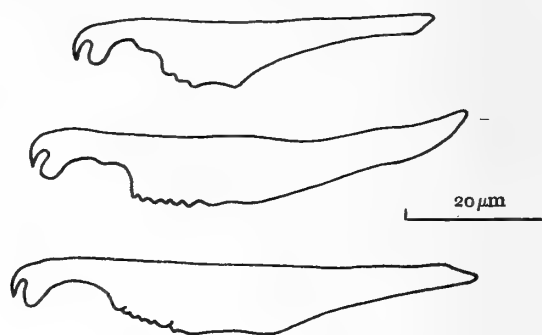


Figure 70

Nitidiscala subcoronata (Carpenter, 1864)

(SBMNH 51501). The bifid structure of the radular teeth is unlike any other thus far reported, with little variation in length. The scale (20 μ m) gives an accurate comparison of teeth size and dentition sculpturing

The radulae of *Nitidiscala subcoronata* and *N. tincta* were extracted by Dr. Eric Hochberg (SBMNH) from dried specimens by soaking in full strength Clorox bleach (sodium hypochlorite). Ribbons were mounted temporarily in glycerin and examined under oil immersion on a Zeiss compound microscope utilizing Nomarski differential interference illumination. Drawings were done with the aid of a drawing tube attached to the microscope. The radulae were permanently mounted in Hoyers Mounting Medium.

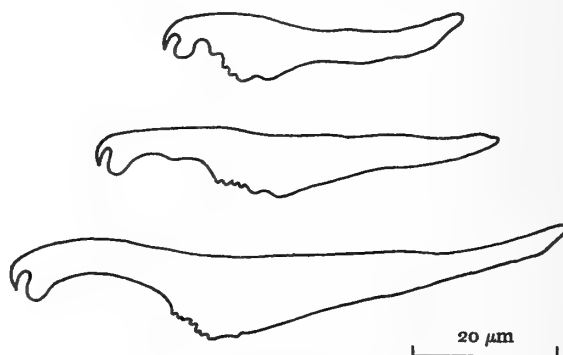


Figure 71

Nitidiscala tincta (Carpenter, 1865)

(SBMNH 21450). Radular slides of Figure 70 and 71 are virtually identical; the larger teeth having a long, smooth blade without projections, the smaller teeth almost always showing projections in this region. (Scale line = 20 μ m)

Geologic Record: Pliocene to Recent.

Lower Pliocene: Towsley Formation, Sand Canyon, off of Santa Clara River Valley (Los Angeles County), LACMIP loc. 291 [4].

Upper Pliocene: Fernando Formation: Sixth and Hope Streets, downtown Los Angeles, LACMIP loc. 466 [106], near Interstate 405 and Cherry Avenue, Long Beach, LACMIP 423 [4] (KENNEDY, 1975: 27). Niguel Formation, Via La Mirada, San Juan Capistrano, LACMIP loc. 4923 [4]. San Diego Formation, Fifth Street, San Diego, LACMIP loc. 323 [5], southwesternmost San Diego County, LACMIP locs. 305 [629], 305-C [159], and 319 [42].

Lower Pleistocene: North of Trinidad at Omenoku Point, LACMIP loc. 3940 [3]. Santa Barbara Formation, bluff on Santa Barbara Yacht Harbor, Santa Barbara, LACMIP loc. 4684 [48]. Rustic Canyon, Pacific Palisades, near Santa Monica, LACMIP loc. 2621 [23]. Baldwin Hills, Los Angeles area, LACMIP loc. 4668 [49], Lomita Marl, in San Pedro, at old Hilltop Quarry, LACMIP loc. 64 [2], and below Host Place and Park Western Drive, LACMIP loc. 435 [544]. Timms Point Silt, Timms Point, San Pedro, LACMIP loc. 62 [1].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP locs. 59 [448] (WILLETT, 1937b: 401, and 4745 [5], near Vermont Avenue and Sepulveda Boulevard, west of Carson, LACMIP loc. 147 [21], Lomita Boulevard and Main Street, Wilmington (Los Angeles), LACMIP loc. 77 [9]. San Pedro Sand, Miraflores Avenue, San Pedro, LACMIP loc. 4565 [7]. Terrace twelve, Palos Verdes Hills, LACMIP loc. 1305 [1] (MARINOVICH, 1976: 23; as *E. sp.*). Formation uncertain, Via Valmonte, Welteria (Torrance), LACMIP loc. 409 [2], and in San Pedro, Pacific Avenue and Oliver Street, LACMIP loc. 131 [1], San Pedro and Wilmington Road, LACMIP loc. 299 [5], and San Pedro waterfront area, LACMIP loc. 1 [6]. West of Interstate 405 and Cherry Avenue, Long Beach, LACMIP loc. 424 [26]. East bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-2 [322] (KANAKOFF & EMERSON, 1959: 27; plus *E. rectilaminatum*), 66-1 [8], 66-9 [1], and 136 [133]. Newport Mesa, west side of "middle" Newport Bay, LACMIP loc. 68-A [specimen missing], and 68-B [1] (KANAKOFF & EMERSON, 1959: 27). Pacific Coast Highway, below Newport Heights, Newport Beach, LACMIP loc. 241 [2]. Calle Fortuna, Capistrano Beach, LACMIP locs. 58 [37] (WILLETT, 1937c [1938a]: 107) and 137 [2]. Near San Clemente RR station,

LACMIP loc. 452 [2]. Bay Point Formation, east side of Mission Bay, San Diego, LACMIP loc. 4562 [3]. South of San Juanico, Baja California Sur, LACMIP loc. 2719 [56].

Recent Records: Forrester Island, Alaska, collected by Willett (1914-1917), one live-taken specimen, DuShane Collection; off British Columbia (23-51° N), collected F. Bernard (1970: 81), intertidal to 20 m; Cape Arago lighthouse, Coos County, Oregon (*Velero III*), among eel grass root masses, July 1942, one specimen (LACM-AHF 1491-42); Depoe Bay, Oregon, collected DuShane, intertidal, one specimen, August 1958, DuShane Collection; Fort Bragg, California, collected DuShane, intertidal in tide pools on anemones, 53 specimens live-taken, August 1965, DuShane Collection; Todos Santos Bay, Baja California Norte, Mexico, collected E. P. Chace, intertidally, 18 specimens live-taken, April 1937, DuShane Collection; Playa San Ramon, Baja California Norte, Mexico (105 miles south of Ensenada), collected DuShane, intertidally, 51 specimens, 1963 and 1967, DuShane Collection; Laguna de San Jose, Baja California Norte, Mexico (Guerrero Negro area), collected DuShane, in tide pools with large anemones, 11 specimens with eggs, February, 1976, DuShane Collection; Magdalena Bay, Baja California Sur, Mexico, collected by Orcutt, March 1917 (USNM 217877).

Discussion: CARPENTER (1864a: 613, 660, 665) referred to *Nitidiscala tincta* as a new species, but gave no description of it until 1865 (p. 31). This species, living intertidally from 0 to 40 m, with a continuous geographical range from Forrester Island, Alaska, collected by WILLETT (1914-1917), to Magdalena Bay, Baja California Sur, Mexico (USNM 217877), collected by Orcutt, is represented by hundreds of stations (LACM) along the California coast. STRONG (1941: 46) believed that the specimens occurring north of Point Conception, Santa Barbara County, California were different enough to allow for a subspecific name, *Nitidiscala tincta subcoronata* (Carpenter).

The lectotype of *Nitidiscala tincta* (PALMER, 1958: 189; USNM 19510), has 8½ whorls, 10 costae, and measures, length 10.5 mm; width 4.5 mm (Figure 48, also figured by STRONG [1930: plt. 20, fig. 3]). The holotype of *Nitidiscala subcoronata* (USNM 14830b), has 1½ nuclear whorls, plus 7 additional ones, 11 costae, and measures, length 13 mm; width 7 mm (Figure 45, also figured by STRONG [1930: plt. 20, fig. 4; incorrect USNM number]). *Nitidiscala continua* (USNM 352383) is synonymous with *N. tincta*, length 8 mm; width 3.6 mm (Figure 47). *Nitidiscala tincta* var. *bormanni* is a small *N. tincta* (Figure 46), as is *N. eelense*. Radulae of *N. tincta* and *N. subcoronata* are virtually iden-

tical. Specimens north of Point Conception, California have larger and heavier shells than those from the south.

Extractions of radular teeth and drawings were made by Dr. Eric Hochberg (SBMNH). Shells and ribbon slides are at the Santa Barbara Museum of Natural History and are: *Nitidiscala tinctoria* (SBMNH 21450), Refugio Beach State Park, Santa Barbara County, California, collected by Gale Sphon, 1965; *Nitidiscala subcoronata* (SBMNH 51501), Fort Bragg, Mendocino County, California, collected by DuShane, 1965 (Figures 70, 71).

Sthenorytis Conrad, 1862

[Type species (SD, De Boury, 1889): *Scalaria expansa* Conrad, 1862]

Whorls rapidly expanding, spire low; costae heavy; basal disk present.

Sthenorytis stearnsii (Dall, 1892)

(Figure 64)

Scala (*Sthenorytis*) *stearnsii* DALL, 1892: 245; pl. 21, fig. 4. Boss, et al., 1968: 304.

Scala stearnsi: STEARNS, 1898: 298. ARNOLD, 1906: 28, 100.

Epitonium (*Sthenorytis*) *stearnsii*: Schuchert, DALL, et al., 1905: 583. DALL, 1908b: 317. GRANT & GALE, 1931: 855. DURHAM, 1937: 482. DUSHANE, 1974: 46, 47.

Original Description: "Shell large, stout, short conical, of about six whorls (the specimen having lost its apex, the exact number is doubtful); each whorl provided with about seven strong reflected varices, slightly angulated near the suture, where each varix is appressed against the interspace and corresponding varix of the antecedent whorl, forming a wave in the varical contour; varices very thick, sharp-

edged, somewhat rugose from the prominence of the incremental lines, on the base overlapping one another and on the spire continuous over the whorls to the apex; surface smooth, except for lines of growth; a faint indication of a basal cingulum is perceptible in one or two of the intervarical spaces; suture filled by the appressed varices; whorls very round, aperture nearly circular, except for the sutural wave. Lon. (of decollate shell $2\frac{1}{2}$ whorls) 26; max. lat. 25 mm" (DALL, 1892: 245).

Additional Description: Shell large, heavy, thick; depressed-turbinate; whorls rapidly enlarging; costae 7, wide, reflected, triangular shaped, each costa flattening as it approaches the suture, joining the costa immediately above, leaving a pit at the suture, broadly reflected on the base, fusing with the lip; suture deep; aperture round, oblique; lip heavy, reflected, continuous; operculum horny, black. Length, 27 mm; width, 24 mm.

Type Material and Type Locality:

Scala (*Sthenorytis*) *stearnsii* Dall: Holotype USNM 106904; Pacific Beach, San Diego, California. San Diego Formation, Pliocene.

Geologic Record: Pliocene (type locality).

Discussion: In more than 80 years there have been no subsequent records of this species from southern California Pliocene deposits. Perhaps Stearns' fossil is an ancestral *Sthenorytis* reaching as far north as San Diego during one of the warm-water phases of the Pliocene. The species is known from only one badly damaged specimen, collected by Stearns from the upper Pliocene San Diego Formation, in Pacific Beach, San Diego, California. However, enough remains to show its affinities to Panamic-Galapagan species of *Sthenorytis* (DUSHANE, 1966: 311; pl. 52, figs. 1-5. 1974: 45-47, figs. 113-117).

Explanation of Figures 60 to 68

Figure 60: *Opalia chacei* Strong, 1937. Holotype, LACM 1045; length, 28.3 mm; width, 10.5 mm × 2.1

Figure 61: *Opalia borealis* Keep, 1881. Live-taken specimen, dredged at 36 m by Willett, off Forrester Island, Alaska; length, 22 mm; width, 7 mm (DuShane Collection) × 2.9

Figure 62: *Opalia spongiosa* Carpenter, 1866. Holotype, USNM 14830; length, 8.5 mm; width, 3 mm × 8

Figure 63: *Opalia retiporosa* Carpenter, 1866. Holotype, USNM 11843; length, 7 mm; width, 2.3 mm × 7

Figure 64: *Scala* (*Sthenorytis*) *stearnsii* Dall, 1892. Holotype, USNM 106904; length, 27 mm; width, 24 mm × 1.4

Figure 65: *Opalia varicostata* Stearns, 1875. Specimen collected by Henry Hemphill [CAS(GTC) 11860], length, 51 mm; width, 27 mm × 1

Figure 66: *Opalia anomala* Stearns, 1875. Specimen collected by Henry Hemphill [CAS(GTC) 11861], length, 37 mm; width, 14 mm × 1.3

Figure 67: *Opalia varicostata* Stearns, 1875. Lectotype, USNM 214040; length, 55 mm; width, 21 mm × 1

Figure 68: *Opalia varicostata* Stearns, 1875. Five specimens (LACMIP) showing gradation from ribbed form to smooth form. Specimens coated with magnesium chloride × 1



Figure 60

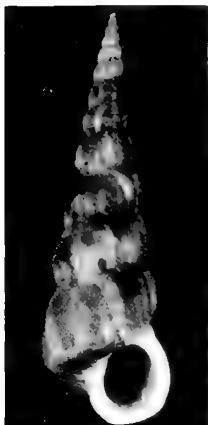


Figure 61



Figure 62



Figure 63



Figure 64



Figure 65



Figure 66

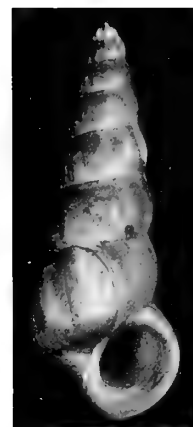


Figure 67

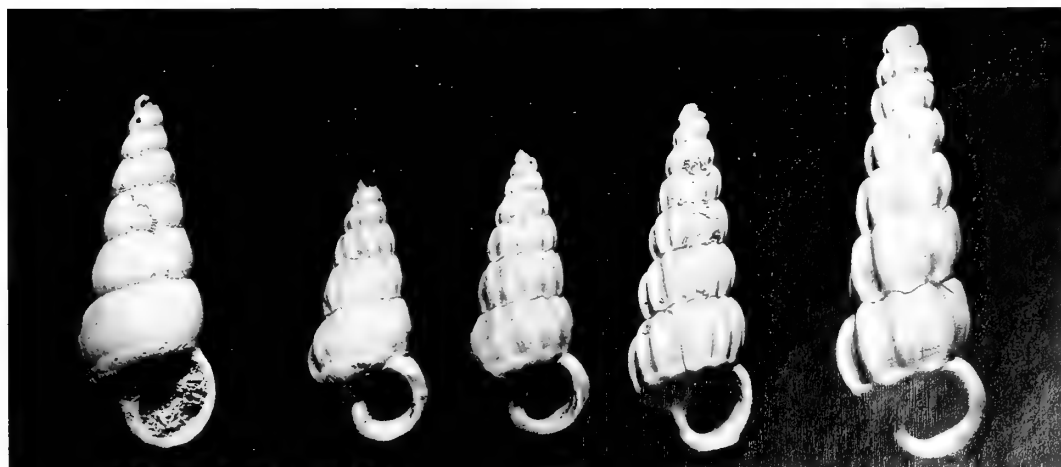


Figure 68

Opalia Adams and Adams, 1853

[Type species: *Scalaria australis* Lamarck, 1822; (SD) De Boury, 1886]

Shells white or light gray to brown in color, solid, imperforate, with axial sculpture of strong ribs that may sometimes be angulated, with or without basal ridge and with spiral sculpture of fine threads between each 2 of which is a row of small pits. Chalky outer layer (intritacalx) over entire shell easily abraded. Oval aperture set at an angle to axis of shell; lip thickened by last axial rib; operculum horny, thin, paucispiral.

Opalia borealis Keep, 1881

(Figures 60, 61)

"*Scalaria borealis* Gould, 1852": [207], of authors. CARPENTER, 1857: 212, 244. REEVE, 1937-1874: plt. 10, fig. 75. TRYON, 1887: 76; plt. 16, fig. 89. R. I. JOHNSON, 1964: 47. [Not of Lyell, 1841.]

"*Opalia borealis* Gould" of authors: CARPENTER, 1864a: 532, 613, 628, 660 [Reprinted, 1872: 18, 19, 114, 146]. CARPENTER, 1865: 31, 32 [Reprinted, 1872: 245]. COOPER, 1870: 67. KEEP, 1881: 28; plt. 6, fig. 5. COOPER, 1888: 255. KEEP, 1893: 49; fig. 30. ARNOLD, 1903: 266. ARNOLD, 1906: 36.

Scala borealis: KEEP, 1904: 201; fig. 212. DEBOURY, 1919: 35.

Scala (Opalia) borealis: BERRY, 1907: 42. BERRY, 1908: 38 [as *Epitonium (O.)*]. KEEP, 1911: 182; fig. 173 [as *Epitonium*].

Epitonium (Acirsa) borealis ("Gould"): KEEP, 1935 ed.: 178 (text only; figure, by error [fig. 52] of *Acirsa borealis* (Lyell)).

Scala Wroblewskyi MÖRCH, 1875: 251 (replacement name for "*S. borealis* Gould" of authors). DEBOURY, 1919: 35.

Scalaria (Psychrosoma) gouldi TAPPARONE-CANEVRI, 1876: 152 (not *S. gouldi* Deshayes, 1861). STRONG, 1937: 4.

Epitonium (Opalia) wroblewskii [sic]: DALL, 1917: 412. DALL, 1921: 113. I. S. OLDROYD, 1924: 108. T. S. OLDROYD, 1925: 13. I. S. OLDROYD, 1927: 51; plt. 31, fig. 5. BERNARD, 1970: 81. ABBOTT, 1974: 115; fig. 1195.

Epitonium wroblewskyi: GRANT & GALE, 1931: 853 (as *E. (Opalia)*). KEEN, 1937, 36. WILLETT, 1937b: 401 (as *E. (Opalia)*).

Opalia wroblewskyi: KEEN, 1937: 43. DURHAM, 1937: 501 (as *O. (Opalia)*). STRONG, 1937: 5; plt. 2, fig. 10 (as *O. wroblewskii* [sic]). BERRY, 1948: 15-19. MORRIS, 1952: 86; plt. 24, fig. 1 (as *O. wroblewskii* [sic]).

Opalia chacei STRONG, 1937: 5; plt. 2, fig. 9. KEEN, 1937: 43. BURCH, 1945: 17. A. G. SMITH & GORDON, 1948: 190. COWAN, 1964: 111. R. I. SMITH & CARLTON, 1975: 489.

Opalia wroblewskyi chacei: EMERSON, 1956b: 338. EMERSON & ADDICOTT, 1958: 9. ADDICOTT & EMERSON, 1959: 16, 21. KANAKOFF & EMERSON, 1959: 29.

Opalia cliacei [sic]: ZINSMEISTER, 1970: 124.

Original Description of *Opalia borealis* KEEP, 1881: "Figure 5, Pl. VI is about an inch long, white, strong, with fewer and blunter ribs than *Scalaria*. It also differs from it by not having a continuous peristome." (KEEP, 1881: 28).

Additional Description: Shell large, with calcareous outer coat (intritacalx), color off-white; nuclear whorls 1½, usually eroded, with axial and spiral sculpture starting on the third whorl down; body whorls 8 to 11, attached at the suture, not rounded, but ascending rapidly, with an acuminate profile; interspaces wider than the ribs; varices usually 7, with here and there a heavier one, particularly on the last 2 whorls, often with a varix continuing beyond the heavy basal ridge onto the base, usually ascending in almost a straight line, one above the other, in older specimens becoming obsolete on later whorls although the basal disk persists; suture distinct but not deep, with a remnant of the earlier basal disk as a small ridge just above the suture line; spiral sculpture of small punctations covering the entire surface of the chalky outer layer, sometimes obliterated on older specimens; lip patulous, peristome coalescing with the parietal wall; operculum brown, horny, with growth lines showing as small ridges on large specimens. Length 6.5 to 43 mm; width 3 to 13 mm.

Type Material and Type Localities:

Scalaria borealis Gould: Holotype missing, probably lost (fide R. I. Johnson, 1964: 47); Puget Sound, Washington.

Scalaria wroblewskyi Mörch: Holotype would be that of *Scalaria borealis* Gould.

Opalia borealis Keep: No definite locality given; figured specimen of Keep, present repository undetermined.

Opalia chacei Strong: Holotype LACM, Section of Malacology 1045; paratypes (6) DuShane Collection; Crescent City, California.

Distribution, Ecology and Bathymetric Range: Forrester Island, Alaska (54°50'N, 133°32'W), with a continuous distribution south to just north of Todos Santos Island, Baja California Norte, Mexico (31°53'20"N, 116°48'15"W). Intertidal to 180m, usually associated with *Anthopleura elegantissima*, among rocks and in tide pools.

Geologic Record: Miocene (?), Pliocene to Recent.

Upper Pliocene: Fernando Formation, Fifth and Hope Streets, downtown Los Angeles, LACMIP loc. 27 [2], east bluff above Upper Newport Bay, Newport Beach, LACMIP loc. 471 [1] (ZINSMEISTER, 1970 [1971]: 124; as *O. cliacei*). San Diego Formation, Market Street, San Diego, LACMIP loc. 127 [2], southwesternmost San Diego County, LACMIP locs. 305 [29, 14 others possibly *O. varicostata*], and 305-A [1 f.].

Lower Pleistocene: Santa Barbara Formation, east of Santa Barbara General Hospital, LACMIP loc. 183-A

[1]. Lomita Marl, in San Pedro, at old Hilltop Quarry, LACMIP loc. 64 [1], and below Host Place and Park Western Drive, LACMIP loc. 435 [34]. Timms Point Silt, Timms Point, San Pedro, LACMIP loc. 130-7 [1].

Discussion: In a Danish paper published early in 1875 (p. 251), MÖRCH proposed a replacement name *Opalia wroblewskyi* for "*Scalaria borealis* Gould (not Beck)" i.e., presumably, GOULD, 1852: 207. Whether Mörch regarded Gould's usage as a misidentification or a homonym is immaterial, for the name was preoccupied by *S. borealis* Lyell, 1841. Mörch's name has priority over *Scalaria (Psychrosoma) gouldi* proposed by TAPPARONE-CANEVRI (1876: 152), which was in turn preoccupied by *S. gouldi* Deshayes, 1861. According to Mörch, Gould thought that *Scalaria australis* Lamarck, 1822, was so similar a species that he withdrew his name. *Scalaria borealis* Gould, 1852 was, in any case, a *nomen nudum*. The replacement name *Opalia wroblewskyi* proposed by Mörch, 1875 was not accompanied by any description or figure; it was based only on the *nomen nudum* of Gould. The first author to give an adequate indication is KEEP, 1881 (p. 178, fig. 152) who used the name *Opalia borealis* for this species [not to be confused with *Acirsa borealis* (Lyell, 1841)]. *Opalia borealis*, as Gould thought, may be similar to *S. australis*, but because of the geographical difference it seems wise to retain Keep's species as distinct, one with a wide distribution in the eastern Pacific, from Forrester Island, Alaska, to near Todos Santos Island, Baja California Norte, Mexico.

No essential differences can be observed between *Opalia borealis* and *O. chacei*. Specimens inhabiting colder waters seem to be longer and slimmer with a more acuminate spire, while those from warmer waters tend to be chunkier, particularly near the basal whorls, ribs slightly wider and rounder and occasionally with one continuous over the low disk, although the relationship of ribs to interspaces is the same. Specimens from off northern California intergrade within the same population.

BERRY (1948: 16), considered *Opalia borealis* Keep and *O. montereyensis* Dall to be closely related. Berry's view seems to be logical even though *O. borealis* has a more acuminate outline, less rounded ribs ascending the spire with more regularity and symmetry, sometimes a heavier rib being carried onto and beyond the basal disk; spaces between ribs twice the width of the ribs. *Opalia borealis* often clusters at the base of the oral disk of the sea anemone *Anthopleura elegantissima* (Brandt), everting its proboscis into the soft base and sucking the body fluids.

Opalia funiculata (Carpenter, 1857)

(Figures 49, 50, 51, 52)

- Scalaria (Cirsotrema) funiculata* CARPENTER, 1857a: 260, 284, 336. CARPENTER, 1857b: 447 [Reprinted, 1967: 447]. HERTLEIN & STRONG, 1951: 89. PALMER, 1951: 62. BRANN, 1966: 17. KEEN, 1968: 408; plt. 57, figs. 50a, b; text fig. 40 (= *Opalia diadema funiculata*).
- Opalia funiculata*: CARPENTER, 1864c: 547, 551 (as *Scalaria* sp.) [Reprinted, 1872: 33, 37]. CARPENTER, 1865: 31 [Reprinted, 1872: 244]. McLEAN, 1969: 34; fig. 2. ABBOTT, 1974: 115; fig. 1198. ABBOTT, 1974: 116; fig. 1202 [*Opalia (Cylindriscala) watsoni* (DeBoury, 1911) as synonym of *O. funiculata*]. McLEAN, 1978: 34; fig. 17.2.
- Not *Scalaria funiculata* WATSON, 1883: 609; ? = *Cylindriscala watsoni* (DeBoury, 1911). [Deep-water, Brazil.]
- Scala funiculata*: ARNOLD, 1903: 267. DeBOURY, 1919: 34, 36.
- Epitonium (Cirsotrema) funiculatum*: KEEN, 1958: 272.
- Opalia diadema funiculata*: KEEN, 1968: 408; plt. 57, figs. 50a-b [fig. 50a: lectotype of *Opalia funiculata*].
- Opalia (Dentiscala) funiculata*: KEEN, 1971: 440; fig. 680. DuSHANE, 1974: 61-63; figs. 122 to 125 and fig. 162.
- Opalia* (? *crenatoides*, var.) *insculpta* CARPENTER 1864c: 539, 619, 660 [reprinted, 1872: 25, 105, 146]. CARPENTER, 1866: 275, 277 [Reprinted, 1872: 322, 324; also reprinted in DALL, 1909: 189]. COOPER, 1888: 255. ARNOLD, 1903: 267. PALMER, 1958: 19, 20.
- Opalia insculpta*: CARPENTER, 1864-65: 10 [Reprinted, 1872: 244]. VAN WINKLE (PALMER), 1921: 4; plt. 1, figs. 10, 11. VALENTINE & MEADE, 1961: 10. ABBOTT, 1974: 115.
- Opalia (Dentiscala) insculpta*: DALL, 1917: 473. STRONG, 1945: 18. PALMER, 1958: 28, 50, 191; plt. 22, figs. 4, 5.
- Epitonium (Dentiscala) insculpta*: BAKER, HANNA & STRONG, 1930: 48. GRANT & GALE, 1931: 855 (as *E. (D.) insculptum*). WILLETT, 1938: 10 (as *E. insculptum*).
- Dentiscala crenimarginata* DALL, 1917: 473. DALL, 1921: 114 (as *E. (Dentiscala)*). KEEN, 1958: 278; fig. 157. PALMER, 1958: 191. McLEAN, 1961: 464. BOSS, et al., 1968: 94.
- Scala crenimarginata*: DeBOURY, 1919: 36.
- Epitonium (Dentiscala) crenimarginatum*: I. S. OLDROYD, 1927: 53. BAKER, HANNA & STRONG, 1930: 47; plt. 2, fig. 6. KEEP, 1935: 180. A. G. SMITH & GORDON, 1948: 190.
- Epitonium crenimarginatum*: KEEN, 1937: 35. WILLETT, 1938: 10. STRONG, 1945: 18.
- Opalia crenimarginata*: THORSON, 1957: 55. ABBOTT, 1974: 115.
- Dentiscala nesiotica* DALL, 1917: 473 [not *Epitonium nesioticum* Dall and Ochsner, 1928]. DALL, 1921: 114 (as *E. (D.)*). STRONG, 1945: 18. BOSS, et al., 1968: 219.
- Scala nesiotica*: DeBOURY, 1919: 37.
- Epitonium (Dentiscala) nesioticum*: I. S. OLDROYD, 1927: 53.
- Epitonium nesioticum*: KEEN, 1937: 35.
- Opalia nesiotica*: ABBOTT, 1974: 115.

Original Description of *Opalia funiculata* (Carpenter): "C. t. subelongata, graciliore, alba; marginibus spirae rectis; anfr. ix. prope suturam valde impressum acute angulatis; costibus variantibus (xv.-xx.) haud acutis, angustioribus, ad angulam coronatis, supra basin vix continuis; anfr. ult. costis plerumque obsoletis, varicibus paucis validis; costa rotundata, suturam continuante, circa basin tumente, a costis radiantibus nodosa; costa spirali altera labio adjacente; tota superficie minutissime decussata; labro a costis sinuato.

"This shell agrees with *C. diadema* in almost every particular down to the minute decussation of the surface. The remarkable pupiform growth of the Peruvian shells however, contrasted with the very regular spire (with one more whirl in proportion) of the Panama and Mazatlan specimens, is thought by Mr. Cuming sufficient to separate the species. The Mazatlan shells are not so large as those in Mr. Cuming's collection, which measure *long.* '7, *long. spir.* '47, *lat.* 34, *div.* 37." (CARPENTER, 1857b: 447).

Additional Description: Shell medium in size, off-white in color; nuclear whorls 3 to 4, usually eroded into a blunt apex; remaining whorls 5 to 7, enlarging rapidly, somewhat rounded, dipping abruptly into a deep suture, ribs 12-16, rounded, following contour of whorl, with an occasional large varix continuing onto the base, strongly developed on top of whorl, appressed to antecedent whorl giving appearance of nodes; ribs almost obsolete on later whorls; interspaces as wide as ribs; punctations fine, between equally fine spiral threads over entire shell, continuing onto base, where they are stronger just below a wide, elevated basal disk, returning to normal as they approach elliptical aperture; lip thick, entire, outer surface concentrically striated, inner lip surface smooth; operculum horny, brown, paucispiral, with about 7 to 9 ridges emanating from nucleus. Length 5 to 17 mm; width 3 to 8 mm.

Type Material and Type Localities:

Scalaria (Cirsotrema) funiculata Carpenter: Lectotype by Keen, 1968 (Panama); paralectotypes (2) (Panama; hypolectotype by Keen, 1968 (Mazatlan); all at BM(NH).

Opalia (?) *crenatoides*, var.) *insculpta* Carpenter: Holotype PRI 7090 [formerly Cornell University 4950]; Santa Barbara, California. Pleistocene, Santa Barbara Formation.

Dentiscala crenimarginata Dall: Holotype USNM 111207; La Paz, Baja California Sur, Mexico.

Dentiscala nesiotica Dall: Holotype USNM 56900; Catalina Island, California.

Distribution, Ecology and Bathymetric Range: From Refugio Beach State Park, Santa Barbara County, California (34°26'N, 120°4'W), with a continuous distribution to the Galápagos Islands, Ecuador, and Tumbes Province,

Perú (3°54'S, 80°53'W). Occurs intertidally down to 30 m; ectoparasitic with sea anemones.

Geologic Record: Pleistocene to Recent.

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP loc. 59 [1]. East bluff above Upper Newport Bay, Newport Beach, LACMIP locs. 66-2 [7] (KANAKOFF & EMERSON, 1959: 29; *O. insculpta*), and 136 [4].

Recent Records:

Opalia funiculata is a common species from California to Peru, so only the most northern and southern points are reported herein: Refugio Beach State Park, Santa Barbara County, California (34°26'N, 120°4'W), collected by Gale Sphon intertidally, four specimens, February 1965 (DuShane Collection). El Rubio and Punta Moro, Tumbes Province, Peru (3°54'S, 80°53'W), intertidally by McLean, Shasky, and Peña, April 1972 (LACM 72-85).

Discussion: *Opalia funiculata* has had many names throughout the years, partly because early workers did not realize the wide geographic range of the species. CARPENTER (1864a: 539) originally considered *Opalia insculpta*, a Pleistocene fossil from Santa Barbara, California, a variety of *Opalia crenatoides* Carpenter. Later he thought *O. insculpta* to be a southern form, but contradicted himself (p.660) when he stated the species is found only as a fossil. He (1866: 275) validated *O. insculpta* by describing it from the "Pleistocene" [= lower Pliocene], explaining that "*Opalia crenatoides* is a recent species with fewer varices than *insculptum* and appears to be quite distinct, though no doubt related."

DALL (1917: 473) described *Opalia crenimarginata* from La Paz, Baja California Sur, Mexico (length 16 mm). Some later workers (see WILLETT, 1938: 10) considered it "identical with Carpenter's earlier *insculptum* and thought the latter name should be used for our recent California species."

DALL (1917: 473) also described *Opalia nesiotica*, dredged in 29 m off Catalina Island, California (length 10.5 mm). Dall separated *O. nesiotica* from other *Opalia* by the sharp spiral sculpture that covered the surface. However, this sculpture is only on the intritacalx, easily abraded and worn off by wave action and rubbing against the substrate.

BAKER, HANNA & STRONG (1930: 47) and A. G. SMITH & GORDON (1948: 190) thought *Opalia insculpta* Carpenter was the fossil form of *Opalia crenimarginata* Dall. The existence of *O. insculpta* at Monterey, California was doubted by SMITH & GORDON (*op. cit.*). PALMER (1958: 191) reported, "The exterior of *O. insculpta* has been worn away

except in the sutural region, [so] the exact character of the longitudinal ribs cannot be described. However, prominent impressions of each reveal 14 ribs on the last whorl." She further questioned Carpenter's reasons for stating there was no spiral sculpture.

Comparisons of the types of these 4 taxa show them to be conspecific (Figure 49, 50, 51, 52). Some of the types are so badly worn that their true relationship to one another was not previously suspected. CARPENTER (1864: 551) stated that the *Scalaria* sp. no. c. reported by C. B. ADAMS (1852) from Panama is *Opalia funiculata*.

KEEN (1968: 408) chose the largest (length 21 mm) of the syntypic specimens of *Opalia funiculata*, from Panama, as lectotype. A specimen with immature lip from Mazatlan (length 16 mm), was selected as hypolectotype.

The radula of *Opalia funiculata* has blunt teeth, short and with a rounded cusp at the center of each tooth in addition to the terminal ones. The broad outline and blunt cusps suggest a carnivorous mode of feeding. *Opalia funiculata* is known to feed on the sea anemone *Anthopleura elegantissima*. The specimen from which the radula was obtained (collected at Palos Verdes Peninsula, California by DuShane), and the radular slide are at the SDMNH.

Opalia infrequens (C. B. Adams, 1852)

(Figures 53, 54, 55, 56, 57)

- Rissoa infrequens* C. B. ADAMS, 1852: 403 [reprinted 1852: 179]. TURNER, 1956: 57; plt. 12, fig. 2. DUSHANE, 1974: 67; figs. 134, 135, 143, 145, 147.
- Opalia (Nodiscala) infrequens* DUSHANE, 1974: 67; figs. 134.
- Epitonium (Pliciscala) infrequens* BARTSCH, 1915: 34.
- Rissoina infrequens* KEEN, 1971: 375, 903.
- Opalia bullata* CARPENTER, 1864c [not *Scalaria bullata* SOWERBY, 1844]: 537, 660 [reprinted, 1872: 23, 146]. CARPENTER, 1865: 397 [reprinted, 1872: 287]. PALMER, 1945: 100.
- Scalaria (Psychrosoma) crosseana* TAPPARONE-CANEVRI, 1876: 154 [replacement name for *Opalia bullata* Carpenter, 1865]. TRYON, 1887: 84.
- Opalia (Nodiscala) bullata*: PALMER, 1958: 20, 23, 50, 192; plt. 22, fig. 6. KEEN, 1971: 440; fig. 681. ABBOTT, 1974: 117.
- Opalia (Dentiscala) mazatlanica* DALL, 1908: 250. DALL, 1917: 474. STRONG, 1945: 19, 21 (*O. (Nodiscala)*). KEEN, 1958: 278 (as *O. (Nodiscala)*). BOSS *et al.*, 1968: 201.
- Epitonium (Nodiscala) mazatlanica*. BAKER, HANNA & STRONG, 1930: 44.
- Scala (Nodiscala) mazatlanica* [sic]: DEBOURY, 1919: 37.
- Opalia tremperi* BARTSCH, 1927: 3; plt. 1, fig. 8. I. S. OLDROYD, 1927: 279. STRONG, 1930: 42. STRONG, 1937a: 7. KEEN, 1946: 8.
- Epitonium (Opalia) tremperi*: GRANT & GALE, 1931: 854.
- Epitonium tremperi*: KEEN, 1937: 36.

Epitonium (Nodiscala) tremperi STRONG, 1945: 19. BURCH, 1945: 19.

Epitonium (Nodiscala) ordenanum LOWE, 1932: 114; plt. 9, figs. 3, 3a.

Opalia (Nodiscala) ordenana: STRONG, 1945: 21. KEEN, 1958: 278; fig. 164.

Original Description of *Opalia infrequens* C. B. Adams: "Shell very long, ovate conic; white; with, on each whorl, sixteen very obtuse slightly elevated indistinct ribs, which are separated only by striae, and a few microscopic revolving striae; apex subacute; spire with the outlines nearly rectilinear; whorls seven, contracted above, otherwise convex or subangular with a moderately impressed suture; last whorl long, subangular; aperture oblique, subovate; scarcely effuse; labrum much excurved, well thickened; umbilicus wanting. Length .24 inch; breadth .075 inch." (C. B. ADAMS, 1852: 403).

Additional Description: Shell small, slim, conic, brown, varying in shading, dead shells white; with soft, calcareous outer coat; nuclear whorls 2, glassy, brown; body whorls 8, evenly punctate between spiral sculpture of small raised threads; suture well defined; ribs 15 to 20, rounded, coalescing at the suture, overlapping at the edge of the preceding whorls to form cusps, with an occasional heavier rib; aperture oval, large; lip strongly expanded and thickened, complete, with the same sculpture as on the whorls; outer lip rounded, inner lip set at an angle against the body whorl; operculum dark, oval, horny, paucispiral, with the nucleus apical. Length 7 to 12 mm; width 2 to 4 mm.

Type Material and Type Localities:

Rissoa infrequens C. B. Adams: Holotype MCZ Harvard 186418; Panama.

Opalia bullata Carpenter: Holotype RM 76, Montreal, Canada; Santa Barbara, California; Pleistocene (Santa Barbara Formation).

Opalia (Dentiscala) mazatlanica Dall: Holotype USNM 168669; Mazatlan, Mexico.

Opalia tremperi Bartsch: Holotype USNM 362454; San Clemente Island, California.

Epitonium (Nodiscala) ordenanum Lowe: Holotype ANSP 157988; San Juan del Sur, Nicaragua.

Distribution, Ecology and Bathymetric Range: From Santa Cruz Island, California (34°03' N, 119°28' W), along the southern California coast to Mazatlan, Mexico, south to Panama. Occurs intertidally to 36 m depths.

Geologic Record: Pleistocene, Recent.

Pleistocene: Santa Barbara Formation, Santa Barbara, California (type locality) [1].

Recent Records: Santa Cruz Island, California (34°03' N, 119°28' W), dredged in shallow water (*teste* KEEN, 1946: 8), SU specimen (now at CAS). South end of

Pulmo Bay, Baja California Sur, Mexico, coarse sand at 20 feet, collected McLean and Oringer, April 1966, one specimen (LACM 66-20). Guatulco Bay, Oaxaca, Mexico, collected Willett, 72-126 m, March 1938, one specimen (LACM A.375). San Juan del Sur, Nicaragua, collected by H. N. Lowe (1931), 36 m, one specimen (as *Epitonium ordenanum*) holotype ANSP 157988. Bahia Herradura, Puntarenas Province, Costa Rica (9°37'58" N, 84°40'30" W), collected McLean, 70 feet, March 1972, one specimen (LACM 72-53). Panama, collected C. B. Adams, one specimen, holotype of *Opalia infrequens*, MCZ 186418.

Discussion: Although C. B. Adams placed his species in the Rissoidae, which later workers followed, BARTSCH (1915: 34) recognized that it belonged in the Epitoniidae and reallocated it in the subgenus *Pliciscala* without commenting on his decision. The type of *Pliciscala* DeBoury, 1887 (Eocene of Europe) has a basal disk and strong axial sculpture that bears little resemblance to the species named by C. B. Adams.

One Pleistocene specimen collected at Santa Barbara by Col. Jewett was first referred to as *Opalia bullata* by CARPENTER (1864: 537, 660), although he did not describe it until 1865 (p. 397). Palmer erroneously thought *O. bullata*, *O. spongiosa* and *O. retiporosa* were conspecific. The latter 2 species, which are probably inseparable, differ from *O. bullata* by having stronger shouldered whorls, ribs that coalesce near the aperture into the basal disk near the aperture, and a less oval aperture. TAPPARONE-CANEFRÌ (1876: 154), believing incorrectly that *O. bullata* was a homonym of *Scalaria bullata* Sowerby, 1844, renamed Carpenter's species *Scalaria (Psychrosoma) crosseana*. TRYON (1887: 84) correctly reinstated *O. bullata*. The type specimen of *O. mazatlanica* DALL (1908: 250) is the largest of the conspecific types; length 12 mm; width 4 mm. No specific diagnostic characters can be found which would differentiate it from *Opalia infrequens*, length 6.5 mm; width 2 mm. *Opalia tremperi* BARTSCH (1927: 3) is here considered to be a synonym of *O. infrequens*. The type is 7.8 mm long and 2.5 mm wide. *Epitonium (Nodiscala) ordenanum* LOWE (1932: 114), has a brown shell with 15 slender ribs; length 7 mm; width 2 mm and is here placed in synonymy.

Opalia montereyensis (Dall, 1907)

(Figures 58, 59)

Scala (Cirsotrema) [sic] montereyensis DALL, 1907: 128. BERRY, 1907: 42. [Not preoccupied by "*Scalaria hellenica montereyensis* DeBoury, 1889" of Palmer, 1958: 190-191, a non-existent name based on a lapsus of DeBoury.]

Epitonium (Cirsotrema ?) montereyensis: DALL, 1917: 477 [not p. 481]. DALL, 1921: 115. I. S. OLDROYD, 1927: 355. GRANT & GALE, 1931: 190.

Opalia montereyensis: STRONG, 1937: 6; plt. 2, fig. 12. KEEN, 1937: 43. BURCH, 1945: 17. BERRY, 1948: 15-19; figs. 1-5. VALENTINE & MEADE, 1961: 10-17. MCLEAN, 1969: 34; fig. 17.3. BERNARD, 1970: 81. R. I. SMITH & CARLTON, 1975: 488. MARINCOVICH, 1976: 6, 12, 23. MCLEAN, 1978: 34; fig. 17.3.

Opalia (Opalia) montereyensis: ABBOTT, 1974: 117.

Scala (Opalia) pluricostata Carpenter MS label: BERRY, 1907: 42 [not *Scala pluricostata* DeBoury, 1913]. PALMER, 1958: 190.

Opalia pluricostata DALL, 1917: 473 [fide BOSS, et al., 1968: 259].

Scalaria pleurocostata [sic] 'Carpenter': STRONG, 1937: 36.

Scala evicta DeBoury, 1919: 36 [new name for *O. pluricostata* Dall].

Epitonium (Opalia) evictum: DALL, 1921: 114. I. S. OLDROYD, 1927: 350. BURCH, 1945: 17.

Opalia evicta: KEEN, 1937: 43. STRONG, 1937: 6; plt. 2, fig. 11. BURCH, 1945: 17. BERRY, 1948: 15. A. G. SMITH & GORDON, 1948: 190. PALMER, 1958: 190; plt. 20, fig. 22 [syn. *O. pluricostata* Dall]. ABBOTT, 1974: 116.

Original Description of *Opalia montereyensis* Dall:

"Shell small (probably not full grown), the nucleus lost but with five subsequent rapidly increasing whorls; shell substance in two layers, the inner translucent white, solid, the outer opaque white, frothy, porous, with numerous punctulations arranged in harmony with the incremental lines; varices low, solid, with a spongy surface, nine in number; basal disk conspicuous, slightly concave; bordered by a conspicuous cord; aperture gibbous, patulous near the imperforate axis. Long. 2.5, diam. 1.5 mm."

"Dredged in 25 fms, mud, off Del Monte, in Monterey Bay, Cala., by S. S. Berry. U.S.N.M. 110431."

"This shell represented by two specimens, of which one is in Mr. Berry's collection, is doubtless immature, but there is no other species known north of Cape St. Lucas belonging to this special group, and, though the characters require rather high magnification to see them clearly, it cannot be confounded with any other Californian species." (DALL, 1907: 128).

Additional Description: Shell small, with calcareous outer coat (intritacalx), color off-white; 1½ nuclear whorls, usually eroded; body whorls 6 to 9, 7 being the usual number, rounded, moderately deep depressions at the junction with the suture, axial ribs 8 to 10, rounded, sometimes disjunct as they ascend the spire; basal disk heavy, joined by the extension of the axial ribs which rarely extend beyond the basal disk; spiral punctations cover the entire shell, about 35 on each whorl, evenly spaced; area below the basal disk concave, making the disk conspicuous; lip quadrate in

outline, aperture round, lip extended anteriorly; operculum horny, brown, paucispiral. Length 2.5 to 16 mm; width 1.5 to 5 mm.

Type Material and Type Localities:

Scala montereyensis Dall: Holotype USNM 110431; para-type (1) S. S. Berry Collection; off Del Monte, Monterey Bay, California.

Opalia pluricostata Dall: Holotype USNM 56054; Neah Bay, Washington.

Distribution, Ecology and Bathymetric Range: From Forrester Island, Alaska (54°50'N, 133°32'W), south to off Vancouver Island, the coasts of Oregon, Washington and California to Cedros Island, Baja California Norte, Mexico (28°20'25"N, 115°11'20"W). This species occurs intertidally among rocks or in tide pools, and may be dredged down to 90 m on rock or among kelp beds.

Geologic Record: Pliocene to Recent.

Upper Pliocene: Fernando Formation, Sixth and Hope Streets, downtown Los Angeles, LACMIP loc. 466 [4], east bluff above Upper Newport Bay, Newport Beach, LACMIP 4956 [1], San Diego Formation, Market Street, San Diego, LACMIP loc. 127 [32], and in southwesternmost corner of San Diego County, LACMIP locs. 305 [430], 305-A [8], 305-C [23], and 318 [3].

Lower Pleistocene: Santa Barbara Formation, Santa Barbara General Hospital, LACMIP locs. 183-A [1], and 183-B [cf. 1 f.].

Upper Pleistocene: Point Arena, LACMIP loc. 4816 [1 f.]. North side of Point Año Nuevo, LACMIP loc. 5019 [2]. Terrace Seven, Palos Verdes Hills, LACMIP loc. 1307 [1] (Marincovich, 1976: 23). Palos Verdes Sand, Vermont Avenue and Sepulveda Boulevard, west of Carson, LACMIP loc. 147 [1]. East bluff above Upper Newport Bay, Newport Beach, LACMIP loc. 66-2 [1 f.] (KANAKOFF & EMERSON, 1959: 29; as *O. wroblewskyi chacei*). Calle Fortuna, Capistrano Beach, LACMIP loc. 58 [1 f.] (WILLETT, 1937[1938a]: 107; as *O. evicta*).

Recent Records: Off Forrester Island, Alaska, collected by Willett (1914-1917) 90 m (USNM 216347). Entrance to Bull Harbor, Hope Island, north end of Vancouver Island, British Columbia, collected by McLean, 15-40 feet, May 1963 (LACM 63-28). Off Cedros Island, Baja California Norte, Mexico, collected by McLean and LaFollette (*Searcher* 231) 15-40 feet, October 1971 (LACM 71-151).

Discussion: DEBOURY (1919: 39) stated that the specific name, "*montereyensis*" was preoccupied, that Dall himself

had used it in 1889 as a subspecies of *Scala hellenica* Forbes (1845: 189). DeBoury apparently misread DALL's (1889: 320-322) *S. hellenica* var. *moerchiana*, an Atlantic species, as "*montereyensis*." There is no usage of "*montereyensis*" by either author in 1889.

Scala (Opalia) pluricostata 'Carpenter,' DALL, 1917 (p. 473), based on a Carpenter MS label name, is synonymous with *Opalia montereyensis*. *Opalia evicta* DEBOURY (1919: 36, 40) is a needless new name for *O. montereyensis*.

The syntypes of *Opalia pluricostata* have much larger shells than *Opalia montereyensis* (length 16 mm; width 5 mm) but have the same number of rounded ribs (8-10), punctate surface, and a conspicuous basal disk. For a more complete discussion see STRONG (1937: 6), BERRY (1948: 16), and PALMER (1958: 190). *Opalia montereyensis* Dall, 1917 should not be confused with *Epitonium montereyense* Dall, 1917, the latter now in the genus *Nitidiscala*.

BERRY (1948: 16) discussed the relationship between *Opalia borealis* Keep and *O. montereyensis*, being of the opinion that the 2 are extremely close allies and that there may exist a geographical gradient from one to the other, an opinion with which I concur. *Opalia montereyensis* has a smaller shell, broader in its proportions, with more compact coiling, a chunkier outline, more deeply and sharply cut relief and a stronger basal disk over which the ribs do not extend. *Opalia borealis* has a more acuminate outline, less rounded ribs ascending the spire with more regularity and symmetry, with sometimes a heavier rib carried onto and beyond the basal disk, and with spaces between the ribs twice the width of the ribs.

Opalia spongiosa Carpenter, 1866

(Figures 62, 63)

Opalia spongiosa CARPENTER, 1864a: 613, 660 [Reprinted, 1872: 99, 146]. CARPENTER, 1865: 31 [Reprinted, 1872: 244]. CARPENTER, 1866: 222. COOPER, 1870: 67. ABBOTT, 1974: 116.

Epitonium (Nodiscala) spongiosum: DALL, 1917: 474. DALL, 1921: 114 (as *E. (N.) spongiosa*).

Epitonium spongiosum: BAKER, HANNA & STRONG, 1930: 44. KEEN, 1937: 35.

Opalia (Nodiscala) spongiosa: STRONG, 1945: 19, 21. PALMER, 1958: 192, 193. KEEN, 1971: 442; fig. 686. DUSHANE, 1974: 68-71; figs. 138, 139.

Opalia retiporosa CARPENTER, 1864a: 613, 660 [Reprinted, 1872: 244]. CARPENTER, 1865: 31 [Reprinted, 1872: 244]. CARPENTER, 1866: 222. DEBOURY, 1919: 34 (as *Scala*). ABBOTT, 1974: 116; fig. 1201. DUSHANE, 1974: fig. 138.

Epitonium (Opalia) retiporosa: MOODY, 1916: 43.

Epitonium (Nodiscala) retiporosum: DALL, 1917: 474. BAKER, HANNA & STRONG, 1930: 45; plt. 2, fig. 3. GRANT & GALE, 1931: 855.

Epitonium (Nodiscala) retiporosa: I. S. OLDROYD, 1927: 53. STRONG, 1945: 19, 21. A. G. SMITH & GORDON, 1948: 190. KEEN, 1958: 278; fig. 165.

Epitonium (Opalia) retiporosum: WILLETT, 1937b: 401.

Epitonium retiporosum: KEEN, 1937: 35.

Opalia (Nodiscala) retiporosa: DURHAM, 1937: 505; plt. 57, fig. 19. KEEN, 1958: 278; fig. 165.

Original Description of *Opalia spongiosa* Carpenter: "O. t. turrita, parva, albida, marginibus spirae rectis; anfr. ix. subplanatis suturis impressis; costis undulantibus circ. xiii., plerumque (nisi ad suturas crenulatus) obsoletis; tota superficie lineis punctorum creberrimis spiralibus, punctis creberrimis, minutis, altissimis; cerca basim imperforatum costa antica latissima, spirali; apertura ovata, valde callosa; operculo auratiaco, paucispirali. Long., 0.36; long. spir., 0.26; lat. 0.12; div. 20°." (CARPENTER, 1866: 222).

Additional Description: Shell brown when live-taken, slender-conic, medium in size; nuclear whorls 2½, glassy, brown; post-nuclear whorls 8 to 9 (southern California specimens tending to have 7 post-nuclear whorls), somewhat rounded; axial and spiral sculpture present over entire shell; ribs 10 to 15, sinuous, prominent, rounded, overlapping the sutures to leave deep pits between, with tubercles at the periphery, more prominent on the last whorl; interspaces as wide as the ribs; sutures deep; spiral rows of punctations over entire shell, about 28 rows on the last whorl, alternate rows smaller in size; basal disk joined by the extensions of the axial ribs to form depressions between; punctate sculpture continuing to the anterior extremity of the shell; aperture subpyriform, set at an oblique angle; lip heavy and reflected on mature specimens, punctate; operculum brown, horny, paucispiral. Length 7 to 13 mm; width 2½ to 5½ mm.

Type Material and Type Localities:

Opalia spongiosa Carpenter: Holotype USNM 14830; Monterey, California.

Opalia retiporosa Carpenter: Holotype USNM 11843; Catalina Island, California.

Distribution, Ecology and Bathymetric Range: Monterey, California (36°37'N, 121°54'W), south into the Gulf of California, and south along the west Mexican coast to the Galápagos Islands, Ecuador (approximately 1°35'S, 80°51'W). Usually dredged on a sand substrate, in from 18 to 72 m.

Geologic Record: Pliocene to Recent.

Upper Pliocene: San Diego Formation, on Market Street, San Diego, LACMIP loc. 127 [2], and in southwesternmost San Diego County, LACMIP locs. 305 [14], 305-A [4], and 305-C [1].

Lower Pleistocene: Lomita Marl, below Park Western Drive and Host Place, San Pedro, LACMIP loc. 435 [36]. Timms Point Silt, Timms Point, San Pedro, LACMIP locs. 62 [1], and 130-7 [4].

Upper Pleistocene: Palos Verdes Sand, Lincoln Avenue, northeast of Playa del Rey (Los Angeles), LACMIP loc. 59 [2] (WILLETT, 1937b: 401; as (*O.*) *retiporosum*).

Recent Records: Off Hopkins Marine Station, Pacific Grove, Monterey, California (36°37.5'N, 121°54'W), collected by McLean, 36 m, 1960, three specimens (LACM 60-23). Off Santa Cruz Island, California, *Velero* III, 67 m, sand and shell substrate, September 1940, two specimens (LACM-AHF 1191 and 1303-41). Coronados Islands, Baja California Norte, Mexico (Pacific side), *Puritan* Expedition, two specimens dredged (AMNH 145: 77775). Maria Madre Island, Tres Marias Islands, Mexico, *Puritan* Expedition, 30 m, one specimen (AMNH 59: 74791). Post Office Bay, Charles Island, Galápagos Islands, Ecuador (approximately 01°15'S, 90°27'W), *Velero* III, bottom sample from 16 m, January 1933 (LACM-AHF 402).

Discussion: Although CARPENTER (1864c: 613) suggested, by implication, the synonymy of *Opalia spongiosa* and *O. retiporosa*, 80 years passed before workers accepted the similarities between the 2 taxa. Unfortunately, Carpenter had very poor specimens from which to make his diagnoses. CARPENTER (1866: 222) states of *O. retiporosa*: "The texture has a rotten appearance; yet one of the specimens was stained with purple, and contained the dried remains of the animal, with its operculum. In the endeavor to extract this, the shell gave way." Carpenter referred to the two species as new several times in his earlier publications before he finally described them in 1866. PALMER (1958: 194) met the "first reviser" rule (ICZN 24A) in discussing *O. spongiosa* and *O. retiporosa*, citing both taxa, considering them to be the same species, relegating *O. retiporosa* to the synonymy of *O. spongiosa*.

Opalia varicostata Stearns, 1875

(Figures 65, 66, 67, 68)

Opalia varicostata STEARNS, 1875: 463; plt. 27, figs. 2-5. DALL, 1878a: 29. DALL, 1878b: 12. COOPER, 1888: 255. DALL, 1892: 245; plt. 21, fig. 4. ARNOLD, 1903: 63, 267. ARNOLD, 1906: 28, 100. DALL, 1917: 473. WOODRING, STEWART & RICHARDS, 1941: 38, 46, 54, 70; plt. 36, fig. 6. WOODRING & BRAMLETTE, 1951: 74, 103, 104; plt. 10, fig. 2. KERN, 1973: 85.

Scala (Opalia) varicostata: DEBOURY, 1919: 36. DURHAM, 1937 [as *Opalia (O.)*]: 502

Epitonium (Opalia) varicostatum: GRANT & GALE, 1931: 853; pl. 24, fig. 20. WILSON, 1966: 112.

Opalia anomala STEARNS, 1875: 464; pl. 27, fig. 1. DALL, 1878a: 29. DALL, 1878b: 12. COOPER, 1888: 255. DALL, 1892: 245. ARNOLD, 1903: 63, 266. ARNOLD, 1906: 28. DALL, 1917: 473.

Scala (Crassiscala) anomala: DEBOURY, 1919: 36.

Epitonium (Opalia) varicostatum var. *anomala*: GRANT & GALE, 1931: 854.

Opalia (Opalia) varicostata var. *anomala*: DURHAM, 1937: 502.

Opalia (Opalia) varicostata var. *granti* DURHAM, 1937: 502; pl. 57, fig. 7.

Opalia varicostata var. *anomala*: WOODRING & BRAMLETTE, 1950: 107.

Original Description of *Opalia varicostata*: "Shell elongated-conical, turreted, tapering, solid, imperforate, aperture ovate, peristome continuous, thickened; dingy to clear white; suture well defined; whorls united, exceedingly variable in convexity and altitude; specimens all decollate, or truncated, equally solid, though varying in length from .75 to 2.45 inches, showing four and one-half whorls within the first measurement to five in the latter. Perfect specimens have probably from 8 to 12 whorls, or even more. Longitudinal ribs 9 to 12, varying in number, prominence, and regularity, as well as in obliquity, when compared with the axial line of the shell, and, in some specimens, irregularly thickened and distorted by the intrusion of a varical rib more or less conspicuously. In some individuals the termination of the rib at the suture gives the upper part of the whorls a crenulated appearance, and the suture in all specimens is more or less waved, dependent upon the prominence of the ribs, which terminate anteriorly at and join a transverse rib at about the middle of the basal whorl.

Number of specimens 22. Collected by Henry Hemphill" (STEARNS, 1875: 463).

Additional Description: Shell heavy, solid, tapering, off-white in color; whorls 10 to 12, variable in convexity; suture well defined; ribs 9 to 12, variable in prominence, regularity and thickness, terminating at the prominent basal disk, with an occasional very heavy one riding over the basal disk and continuing to the oval aperture; peristome thick, continuous. Length 20 to 60 mm; width 14 to 20 mm.

Type Material and Type Localities:

Opalia varicostata Stearns: Lectotype (USNM 214040a), selected herein; length, 55 mm; width, 21 mm. Paralec-
totypes (3) (USNM 214040b), designated herein; Pacific Beach, San Diego, California (Pliocene, San Diego Formation).

Opalia anomala Stearns: Holotype USNM 214041; same locality as above.

Opalia varicostata var. *granti* Durham: Holotype UCMP 30166; Pacific Beach, California (Pliocene, San Diego Formation).

Distribution, Ecology: Extinct species from Wishkah River, Washington, Zapata Creek, Fresno County, California, Los Angeles and San Diego Counties, California, and northern Baja California Norte, Mexico.

Geologic Record: Note: The number of specimens of the variety *anomala* is followed by "a" in brackets following each locality.

Lower Pliocene: Towsley Formation, Sand Canyon, off Santa Clara River Valley (Los Angeles County), LACMIP loc. 291 [2].

Upper Pliocene: Temescal Canyon, Pacific Palisades, LACMIP locs. 42 [1], and 4472 [1]. Niguel Formation, Via La Mirada, San Juan Capistrano, LACMIP loc. 4923 [4a]. San Diego Formation, in San Diego, at end of Loring Street, Pacific Beach, LACMIP loc. 122 [180; 29a], Diamond Street, Pacific Beach, LACMIP loc. 4523 [8], end of Arroyo Drive, Pacific Beach, LACMIP loc. 107 [6; 2a], near Wabash Boulevard and Gateway Drive, LACMIP loc. 1187 [1], on Market Street, LACMIP loc. 127 [2], San Diego "area," LACMIP loc. 4758 [4; 2a], southwesternmost San Diego County, LACMIP locs. 305 [28; 17, 1 f. a], 305-A [1; 22a], 305-C [2], 318 [2a], and 319 [5a]; in Baja California Norte, 4½ miles south of U.S. border on old coast highway, LACMIP loc. 449 [2 f.], La Joya turnoff on Mexico Highway 1-D, south of Tijuana, LACMIP loc. 4755 [1].

Discussion: This Pliocene fossil seems to be common in the San Diego, California area, having been reported by many authors. The most northerly occurrence is reported by DURHAM (1937: 502) at Wishkah River, Washington from the upper Miocene or lower Pliocene, Montesano Formation.

Opalia anomala, described by STEARNS (1875: 464) as a variety of *O. varicostata* grades directly into the latter through the gradual obsolescence of the longitudinal ribs, except on the spire, where axial sculpture is often present. As a variety it is of little value. DEBOURY (1919: 36) erroneously placed *O. anomala* in the subgenus *Crassiscala*, although he conceded that *O. varicostata* belonged in *Opalia*.

DURHAM (1937: 502) named the variety *O. varicostata* var. *granti*, from the Pliocene San Diego Formation, in Pacific Beach, California, with 8 axial ribs, and a thin, high spired shell of 9 whorls.

EPITONIIDAE OF DOUBTFUL STATUS

Epitonium (Nitidiscala) crebricostatum (Carpenter, 1864)

Scalaria crebricostata CARPENTER, 1864: 613, 660 [Reprinted, 1872: 99, 146]. CARPENTER, 1866: 222. COOPER, 1870: 67. KEEF, 1881: 28; pl. 6, fig. 4 (*E. tinctum*). COOPER, 1888: 263. KEEF, 1911: 184.

Scala crebricostata: ARNOLD, 1903: 263. KEEF, 1904: 202. ARNOLD, 1906: 36. STRONG, 1930: 188.

Epitonium crebricostatum: DALL, 1917: 478. T. S. OLDROYD, 1925: 13. ABBOTT, 1974: 119.

Epitonium (Nitidoscala) [sic] crebricostata: DALL, 1917: 478. DALL, 1921: 115. I. S. OLDROYD, 1924: 108. I. S. OLDROYD, 1927: 61.

Epitonium (Nitidiscala) crebricostata: KEEF, 1935: 180. STRONG, 1945: 24.

Epitonium (Nitidiscala) crebricostatum: GRANT & GALE, 1931: 858; pl. 22, fig. 11. KEEN, 1937: 35. STRONG, 1945: 26. BURCH, 1945: 29. A. G. SMITH & GORDON, 1948: 191. KEEN, 1958: 274. PALMER, 1958: 184; pl. 20, figs. 27-28.

Description of *Scalaria crebricostata* CARPENTER (1864: 660): "Mus. Cuming no. 32: 15 sharp, reflexed ribs, coronated against the sutures."

Description of *Scalaria crebricostata* CARPENTER (1866: 222): "S. t. gracili, tenui, alba; anf. x. rotundatis, haud attingentibus; costis circ. xv., acutis, reflexis, vix attingentibus, lineis irregulariter spiralibus ascendentibus; costis juxta suturam eleganter coronatis; sculptura spirali, nisi striulis interdum exillimis, nulla; aperture rotundata; umbilico nullo; operculo normali, dense corneo. Long. 0.70; long. spir. 0.52, lat. 0.18, div. 26 [length 17.71 mm; width 4.55 mm]."

Hab. Monterey, San Pedro, Cooper, common.

= "*Scalaria*, unique" Mus. Cum. No. 32.

Somewhat resembles *S. tenuis*, Sby., but is not so turritid."

Material and Localities:

BM(NH), Registry 1950. 3. 29. 1, one specimen labelled "California," 12 costae, length 9.7 mm; width 3.6 mm.

USNM 46234 [ex 14831]. Recatalogued in 1885, labelled "Type-Monterey-Cooper," 3 live-taken specimens:

11 costae, length 16 mm; width 8.5 mm

10 costae, length 9 mm; width 4 mm

7 costae, length 8.5 mm; width 4 mm

Discussion: Through the years *Scalaria crebricostata* Carpenter has been an enigma to workers. None of the specimens extant at the BM(NH), and the USNM match the descriptions given by CARPENTER (1864: 660; 1866: 222). Inasmuch as Carpenter's brief description (1864) and detailed description (1866) specify a shell of dimensions different from those of the one specimen in the BM(NH), one can only assume that the original specimen is lost. None of the

specimens at the USNM can qualify because their dimensions are far different from the descriptions given by Carpenter. Because of the uncertainty of the identity of Carpenter's taxon it is here rejected as a *species inquirenda*. The specimens at the USNM labelled "*crebricostata*" are *Nitidiscala caamanoi* (Dall and Bartsch, 1910).

REJECTED RECORDS

Epitonium (Asperoscala) [sic] arnoldi Dall, 1917

The description given by DALL (1917: 475), type locality San Pedro, California (length, 14 mm; width, 5.5 mm), parallels that given by CLENCH & TURNER (1952: 292) for *Epitonium (Asperiscala) multistriatum* (Say, 1826). Comparison of the holotype of *E. arnoldi* Dall (USNM 106875), with photographs of the type of *E. multistriatum* (Say) confirms the opinion that the description of *E. arnoldi* is based on specimens of *E. multistriatum* (Say) with an erroneous locality label. On the Atlantic coast the range is from Buzzards Bay, Massachusetts south to Cape Canaveral (Cape Kennedy), Florida.

Epitonium (Nitidoscala) [sic] barbarinum Dall, 1919

The holotype of *Epitonium (Nitidoscala) [sic] barbarinum* Dall, 1919 (USNM 46229) from the Stearns collection, type locality, San Diego, California, is a specimen of *Epitonium angulatum* (Say, 1830), with a range on the Atlantic seaboard and in the Gulf of Mexico, from Long Island, New York south to Florida (excluding the Florida Keys) and west to Texas. DALL (1921: 116) gave the range for *E. barbarinum* from San Diego, California to Panama. Moreover, Dall's original measurements (length 19 mm; width 6.5 mm) are in error. The type of *E. barbarinum* has been measured several times by Joseph Rosewater (USNM) and DuShane: length 13.9 mm; width 6 mm, within the size range for *E. angulatum*. Thus, *E. barbarinum*, as a species, is eliminated from the eastern Pacific fauna, and was renamed as a previously misidentified species from the upper Gulf of California, Mexico (DUSHANE, 1979: 379).

Epitonium (Nitidiscala) hexagonum (Sowerby, 1844)

Originally described by SOWERBY (1844: 98) (four syntypes: BM(NH)), from Acapulco, Mexico, this species is not known north of Magdalena Bay, Baja California Sur (SDMNH Collection), collected by Orcutt, 1917. There are several records of beachworn shells, from California and

Baja California, dating from the turn of the century; USNM 221848 and USNM 221849, Santa Cruz, California (Button); USNM 211020, Ocean Beach, California (Cook); USNM 105506, Scammon's Lagoon (Hemphill). It is possible that the species had a more extensive distribution at that time; however, until live-collected specimens are known from this region, the species is not regarded as a member of the fauna. The range is from Magdalena Bay, Baja California Sur, and the west side of the Gulf of California, Mexico; disjunct to Acapulco, Mexico, then south to Panama.

Epitonium lagunarium Dall, 1917

Known only from the holotype (USNM 253024), type locality Laguna Beach, California, there have been no subsequent reports of this taxon from the eastern Pacific. DALL's (1917: 477) description matches well the description of *Epitonium rupicolum* (Kurtz, 1860), and examination of the type of *E. lagunarium* confirms the opinion. *Epitonium rupicolum* is a common species from Massachusetts to Texas.

Epitonium tiara (Carpenter, 1856)

DALL's record (1917: 480) of *Epitonium tiara* Carpenter, ranging from Catalina Island, California to Todos Santos Bay, Baja California Norte (repeated by I. S. OLDROYD (1927), KEEN (1937), and BURCH (1945)) was a misidentification, as the taxon is synonymous with *Asperiscala obtusa* (Sowerby, 1844) (DUSHANE, 1974: 22), a species ranging from the Gulf of California south to Colombia.

Epitonium zephyrium Dall, 1917

The United States National Museum has two specimens labelled "*Epitonium zephyrium*" (USNM 56056 and USNM 635572). Neither specimen matches the description given by DALL (1917: 485) who stated, "without basal disk or cord." Both USNM specimens have a basal cord and neither has the dimensions given by Dall in his original description. Dall did not figure the specimen. One can only conclude that the holotype is now lost. No other specimens of *E. zephyrium* seem to be in museum or private collections. The two specimens at the USNM are *Epitonium lamellosum* (Lamarck, 1822), which has been reported along the shores of Australia, Japan, southern Europe, western, southern, eastern Africa, eastern coast of the United States from Florida and the Gulf of Mexico south to eastern Colombia.

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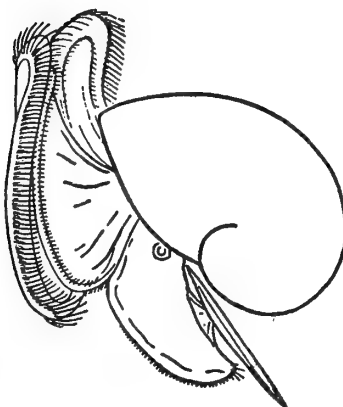
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On the Growth Stages of *Conus fergusonii* Sowerby, 1873,
the Reinstatement of *Conus xanthicus* Dall, 1910,
and a New Species of *Conus* from the Galápagos Islands

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(3 Plates; 4 Text figures)

INTRODUCTION

IN REVIEWS OF EASTERN PACIFIC *Conus* species, NYBAKKEN (1970: 25; 1971: 97) reported markedly different radula morphology between specimens considered adults and juveniles of *C. fergusonii* Sowerby, 1873. Nybakken suggested 3 possible explanations for this apparent anomaly: 1) dimorphism in *C. fergusonii*, 2) change in radula morphology with growth, 3) confusion between 2 species. Too few specimens were then available to allow resolution of the problem. Since that time additional specimens have enabled us to reach new conclusions.

Mature specimens of *Conus fergusonii*, largest of the tropical eastern Pacific species of *Conus*, have readily been recognized by previous workers. The juvenile shell of the species has not been understood, however. Recent authors (HANNA & STRONG, 1949; KEEN, 1958; EMERSON & OLD, 1962; HANNA, 1963; NYBAKKEN, 1970, 1971; KEEN, 1971) have considered the taxon *C. xanthicus* Dall, 1910, to represent the immature form of *C. fergusonii*. We now show that *C. xanthicus* is separable from *C. fergusonii* on both shell and radula morphology. The true juvenile of *C. fergusonii* is described and figured for the first time.

During this study, we found that some specimens from the Galápagos Islands thought to be *Conus xanthicus* had a radula unlike that of either *C. xanthicus* or *C. fergusonii*. We describe these specimens as a new species, *C. kohni* McLean & Nybakken.

In this account we give comparative descriptions of the 3 taxa and figure a number of specimens to illustrate growth stages and some of the variation in each species. We have examined all previously illustrated specimens in the California Academy of Sciences and the American Museum of Natural History collections. The figure citations in our synonymies are based upon new determinations of the identity of these specimens. Our radular descriptions employ the terminology used by NYBAKKEN (1970). The accounts of the radula are based on the following number of examined specimens: *Conus fergusonii* 5, *C. xanthicus* 10 (including the holotype); *C. kohni* 6 (including the holotype).

Museum abbreviations used in the text are as follows: AHF, Allan Hancock Foundation, University of Southern California (collection housed at LACM); CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; USNM, United States National Museum of Natural History, Washington.

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We are especially grateful to Mr. Leroy H. Poorman, Westminster, California, who was much involved in the discussions that led to the recognition of the growth stages of these species. He has also donated specimens (Figures 6, 11, and 15) important to this work. Mr. Gerald Wellington, University of California, Santa Barbara, contributed specimens

from the Galápagos Islands, including the type lot of the new species. Additional specimens have been loaned by Mr. Alex Kerstitch of Tucson, Arizona. We thank curators and staff at the American Museum of Natural History, California Academy of Sciences, and the National Museum of Natural History for the loan of the specimens.

William K. Emerson, A. Myra Keen, Alan J. Kohn, Patrick I. LaFollette, and Leroy H. Poorman critically read the manuscript and offered helpful suggestions. We are grateful to Dr. Kohn for allowing us to compare the new species with his collection of type photography, specimens, and radula slides. The photographs are the work of Mr. Bertram C. Draper, Los Angeles.

SPECIES ACCOUNTS

Conus fergusonii Sowerby III, 1873

(Figures 1, 2, 5-11)

Conus fergusonii SOWERBY III, 1873: 145; plt. 15, fig. 1 - 1887: 256; plt. 508, fig. 675 - DALL, 1910: 218 - HANNA & STRONG, 1949: 294; plt. 7, fig. 3 - KEEN, 1958: 485; fig. 938 - EMERSON & OLD, 1962: 26; fig. 14 - HANNA, 1963: 42; plt. 4, fig. 2; plt. 9, fig. 10 - NYBAKKEN, 1970: 13; figs. 18, 19 (radula), figs. 40, 41 - NYBAKKEN, 1971: 97; fig. 4 - KEEN, 1971: 667; fig. 1511 left.

Diagnosis: Coronations persisting through 10th whorl, spire whorls slightly concave; large specimens white, small

specimens yellow-orange, with lighter, even banding; shells under 25 mm in length with widely spaced spiral rows of dark brown spots; spire lacking color pattern.

Description: Shell large (maximum length 153 mm, with 12 to 13 teleoconch whorls); spire low to moderately elevated; spire outline concave in small specimens to nearly straight in large specimens; shoulder sharply angulate in small specimens, less angulate in large specimens; the angulation with low coronations in small specimens, the coronations often persisting through a shell length of 50 mm; coronations indistinct and undulating in large specimens; spire whorls slightly concave, spire sculptured with fine spiral striae and growth lines; suture produced at the shoulder, deeply and narrowly incised; whorl profile more or less straight except convex below the shoulder; surface smooth except for 10-15 spiral striae on lower third of whorl; aperture moderately broad, of about the same width throughout and conforming to whorl profile. Protoconch homeostrophic, 3-whorled, smooth, dark; shoulder of early teleoconch whorls angulate; suture produced well below the angulation; suture rising to meet the shoulder by the 6th whorl; coronations on the shoulder angulation persisting to at least the 8-whorled stage. Color light yellow-orange, paler in medium-sized specimens, fading to white in large specimens; small specimens with a distinct lighter spiral band about the middle of the shell and usually a second light band at the shoulder; spire lacking color pattern; small specimens with spiral rows of dark brown dots on body whorl; aperture white within. Periostracum thin

Explanation of Figures 5 to 12

(Figures are scaled to render a shell 60 mm in length at life size and a 15 mm shell at a length of 35 mm, with intermediate-sized shells proportionally scaled. Spire views are oriented perpendicular to a plane touching the apex and the shoulder and are enlarged to a diameter of 2/3 the length of the frontal view.)

Conus fergusonii Sowerby III, 1873

Figure 5: AHF 395-35, 26-29 m, rocky, off Isla Lobos de Afuera, Peru. Radula verified specimen, length 61 mm, periostracum intact.

Figure 6: LACM 35506, 73 m, muddy, Bahía Bocochibampo, Guaymas, Sonora, Mexico. Length 52.6 mm, periostracum removed (spire with persistent coronations; largest specimen examined showing juvenile spotted pattern).

Figure 7: LACM 72-73, 40-55 m, Golfo Dulce, Puntarenas Prov., Costa Rica. Length 52.4 mm, periostracum intact (spire coronations relatively faint).

Figure 8: AHF 431-35, 82 m, sand & gravel, off Rocas Octavia, Colombia. Radula verified specimen, length 43.5 mm, periostracum intact (spire coronations prominent).

Figure 9: CAS 12310, 77 m, off Punta Judas, Costa Rica. Length 42.8 mm, periostracum removed from body, intact on spire (spotted specimen figured by HANNA, 1963, plt. 9, fig. 10).

Figure 10: LACM 72-12, 53-26 m, mud, Bahía Elena, Guanacaste Prov., Costa Rica. Radula verified specimen (see Figure 2), length 26.1 mm, periostracum removed (spotted juvenile; smallest radula-verified specimen).

Figure 11: LACM 36563, 20 m, Bahía Santiago, Colima, Mexico. Length 14.0 mm, dead specimen, periostracum worn away (spotted juvenile, smallest specimen examined).

Conus virgatus Reeve, 1849

Figure 12: CAS 39174, vicinity of Guaymas, Sonora, Mexico (from shrimp boats). Length 41 mm, periostracum removed, surface eroded (example of banded form; note lack of coronations; specimen previously misidentified as *C. fergusonii*).

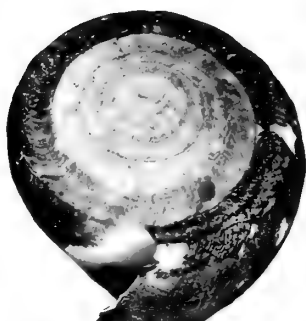


Figure 5



Figure 6

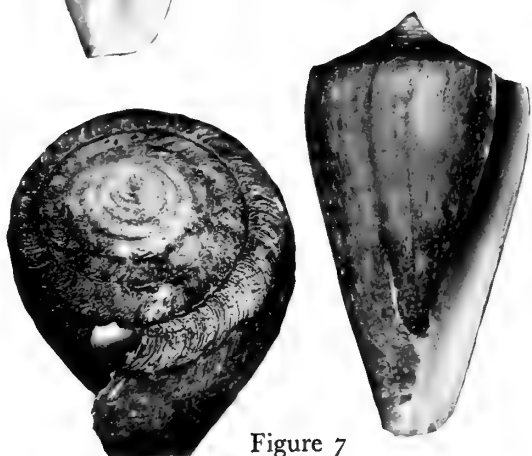


Figure 7



Figure 8



Figure 9

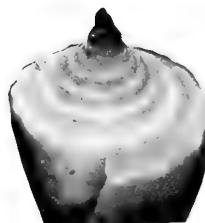


Figure 10

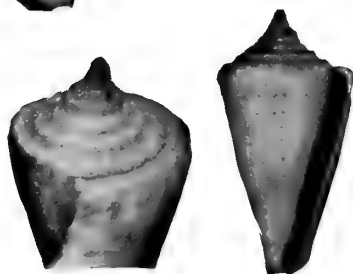


Figure 11

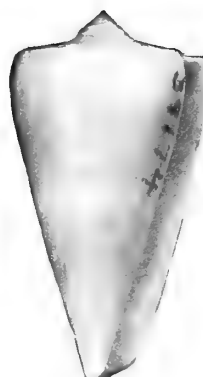


Figure 12

and light colored in small specimens, thick and dark brown in large specimens, produced in closely set, concave ridges on the spire. Operculum bluntly unguiculate, about 4 times longer than wide.

Radula (Figures 1, 2): Tooth from mature specimens

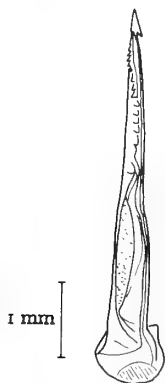


Figure 1

Conus fergusonii, from 26.1 mm specimen (shell: Figure 10).
Radular tooth (scale = 0.1 mm)

(Figure 2) long; serration extending half the length of the tooth, terminating proximally in a pointed or rounded cusp; barbs 2, one at the tip, the other on the opposite side; blade and waist lacking, base enlarged, rounded, bearing a pointed spur. Tooth from the smallest specimen examined (Figure 1) (shell length 26.1 mm, Figure 10), proportionately shorter, the 1st barb weaker, 2nd barb undeveloped; waist indistinct, the proximal portion of the shaft wider than the distal; base enlarged, rounded, with prominent spur.

Radula preparations were made from 5 specimens, including those illustrated in Figures 5, 8, and 10. Except for the radula from the smallest specimen (Figure 10), there was no significant variation in tooth morphology.

Distribution and occurrence: Bahía Tortuga, Baja California, Mexico (HANNA & STRONG, 1949), north in the Gulf of California to Guaymas, Sonora, south to Isla Lobos de Afuera, Peru; Galápagos Islands, Ecuador. *Conus fergusonii* is uncommon at the Galápagos Islands; we have received specimens collected by Gerald Wellington at Isla Isabela and HANNA & STRONG (1949) mentioned a specimen of 128 mm in length collected at Caleta Tagus, Isla Isabela. Near the northern and southern range extremes, the entrance to Bahía Magdalena, Baja California, Mex-

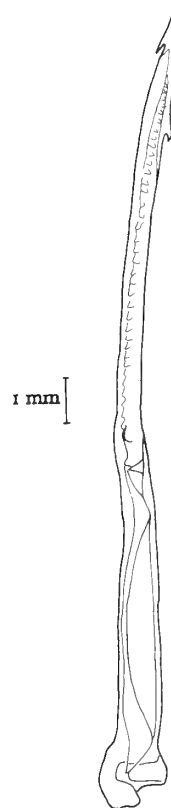


Figure 2

C. fergusonii, from 51.9 mm specimen (Gulf of Panama, Univ. of Miami, uncatalogued).

Radular tooth (scale = 0.1 mm)

ico, in the north, and Isla Lobos de Tierra and Isla Lobos de Afuera, Peru, in the south. McLean observed *C. fergusonii* on rocky bottoms at shallow subtidal depths. At localities in the central part of the range it is less common and is known only from dredged records. The species is not restricted to a rocky substrate; McLean has observed large numbers taken on soft bottoms on the shrimp fishing ground in the Gulf of Guayaquil off northernmost Peru.

Comparisons: Immature specimens of *Conus fergusonii* differ from *C. xanthicus* and *C. kohni* in having prominent coronations on the early whorls. The coronations persist through at least the 8-whorled stage and may be observed in spire view on specimens of any size, including shells with

intact periostraca. Similar persistent coronations characterize *C. patricius* Hinds, 1843, but that species differs in having a rounded shoulder and a marked concavity of the lower body whorl profile, features particularly apparent in young shells. The color patterns of young shells of *C. fergusoni* differ from those of both *C. xanthicus* and *C. kohni* in lacking mottling on the spire and in having even banding, and in younger stages, rows of dark spots, instead of mottled banding with jagged edges.

An uncommon color form of *Conus virgatus* Reeve, 1849, has also been a source of confusion. This form, an example of which was described as *C. signae* Bartsch, 1937, lacks axial flammules and may have a central band of lighter color intensity. However, such specimens of *C. virgatus* (Figure 12) lack coronations on the spire and the whorls are not as rapidly expanding as in *C. fergusoni*.

Variability: *Conus fergusoni* is moderately variable in shell proportion and height of spire. For example, shells in Figures 6 and 7 are of about the same length but that in Figure 6 is lower spired, broader at the shoulder and has a more pronounced bulge below the shoulder. Young shells lose the typical coloration of banding and spotting at different sizes. All of the 5 smallest shells examined (none exceeding 26 mm in length) are spotted. Spots have been observed on one shell as large as 52.6 mm in length (Figure 6); the smallest shell observed on which spots are lacking is 43.5 mm in length (Figure 8).

Remarks: The original illustration of *Conus fergusoni* is an accurate rendition of a large, white-shelled specimen lacking the periostracum, 145 mm in length, apparently life size, no dimensions being given. The description consisted of a brief Latin diagnosis. The source of the original material was given as follows: "Several specimens . . . collected at Panama by Mr. Ferguson." The present location of type material is unknown; specimens have not been located in the British Museum (Alan J. Kohn, personal communication).

Previous accounts of *Conus fergusoni* have included *C. xanthicus* Dall, 1919, as a synonym, thereby attributing excessive variability to the species. This confusion is no doubt due to scarcity of juvenile specimens of *C. fergusoni*. In all the museum and private collections examined by us, we have located only five specimens under 40 mm in length. McLean can attest to the apparent absence of juveniles, having seen numbers of mature specimens at Isla Lobos de Afuera, Peru, but none under 55 mm in length, despite having taken many gravel samples from crevices and under rocks.

HANNA & STRONG (1949: 295) and HANNA (1963: 43) claimed that "a magnificent series of growth stages has enabled us to state with assurance that *C. xanthicus* is the young of *C. fergusoni*." We have examined all small specimens in the California Academy collection previously identified as *C. fergusoni* and find that the smallest authentic specimen studied by Hanna is the 42.8 mm shell figured in

Explanation of Figures 13 to 23

Conus xanthicus Dall, 1910

- Figure 13: USNM 111236, Holotype of *C. xanthicus*, 130 m, sand, off Guaymas, Sonora, Mexico. Radula verified specimen, length 42.5 mm, periostracum removed.
- Figure 14: Berry Collection, Holotype of *C. chrysocestus*, 55-82 m, off Morro Colorado, Sonora, Mexico. Length 45.3 mm, periostracum removed (relatively low-spired specimen).
- Figure 15: LACM 11345, 73 m, off La Paz, Baja California, Mexico. Radula verified specimen, length 53.4 mm, periostracum removed (relatively low-spired specimen).
- Figure 16: AHF 1118-40, 108-126 m, coarse gray sand, Banco Gorda, Baja California, Mexico. Length 40.0 mm, periostracum removed on ventral side, intact on dorsal side (relatively high-spired specimen).
- Figure 17: CAS 17809, 29 m, Bahía Chamela, Jalisco, Mexico. Length 41.9 mm, periostracum intact (relatively low-spired specimen; spiral sculpture on spire whorls especially prominent).
- Figure 18: AHF 300-34, 73 m, sand, Bahía Azufre, Isla Clarion, Revillagigedo Islands, Mexico. Radula verified specimen, length 24.3 mm, periostracum removed.
- Figure 19: AHF 431-35, 82 m, sand & gravel, off Rocas Octavia, Colombia. Radula verified specimen, length 39.1 mm, periostracum removed (relatively slender specimen).
- Figure 20: AHF 325-35, 146 m, rocky, Caleta Tagus, Isla Isabela, Galápagos Islands, Ecuador. Length 46.8 mm, periostracum removed (largest specimen examined from Galápagos Islands).
- Figure 21: AHF 792-38, 128-146 m, off Isla Daphne Chica, Galápagos Islands, Ecuador. Radula verified specimen, length 35.7 mm, periostracum intact.
- Figure 22: CAS 38975, 18-37 m, off Isla Rabida, Galápagos Islands, Ecuador. Length 32.2 mm, periostracum removed.
- Figure 23: AHF 324-35, 82 m, rock, Caleta Tagus, Isla Isabela, Galápagos Islands, Ecuador. Radula verified specimen, length 14.3 mm, periostracum partially intact (smallest specimen examined).

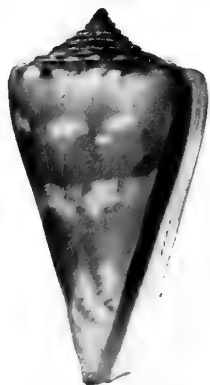


Figure 13



Figure 14



Figure 15

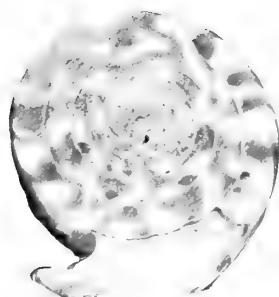


Figure 16



Figure 17



Figure 18



Figure 19



Figure 20

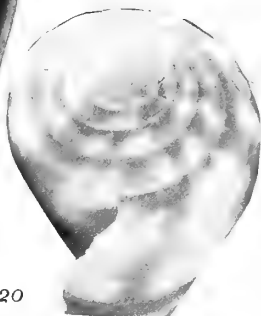


Figure 21

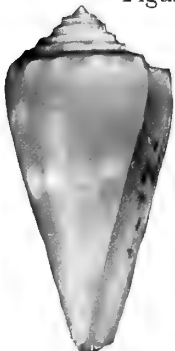
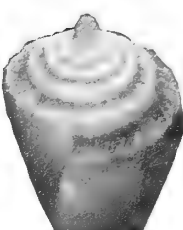


Figure 22



Figure 23



color (HANNA, 1963: plt. 9, fig. 10), our Figure 9. Other small specimens in the Academy collection are identified by us as *C. xanthicus*. There is no indication of intergradation with *C. fergusonii*. EMERSON & OLD (1962: 27) considered specimens resembling *C. xanthicus* "to be merely a highly colored deep water ecotype of *C. fergusonii*," but did not document any depth-related distinctions. They noted coronations in the one authentic specimen of *C. fergusonii* they illustrated but did not question the lack of this character in the other specimens so identified.

Conus fergusonii is one of few species in which a young specimen of *Conus* has been shown to have a radular tooth morphology differing from that of the adult. We treat this further in the discussion section of this paper.

Conus xanthicus Dall, 1910

(Figures 3, 13-23)

Conus xanthicus DALL, 1910: 225 - HANNA & STRONG, 1949: 294 (as syn. of *C. fergusonii*), plt. 7, figs. 1, 2, 4 (holotype) - KEEN, 1958: 485 (as syn. of *C. fergusonii*) - EMERSON OLD, 1962: 26 (as syn. of *C. fergusonii*), figs. 13 left, 13 right, 15 left, 15 right - HANNA, 1963: 42 (as syn. of *C. fergusonii*), plt. 2, fig. 4, plt. 5, fig. 5 (holotype), plt. 7, fig. 9 - NYBAKKEN, 1970: 25 (status uncertain); fig. 20 (radula), figs. 42, 43 - NYBAKKEN, 1971: 97 (as possibly valid species); fig. 5 - KEEN, 1971: 667 (as syn. of *C. fergusonii*); fig. 1511 right (holotype of *C. chrysocestus*).
Conus chrysocestus BERRY, 1968: 157 - NYBAKKEN, 1971: 99 (as syn. of *C. fergusonii*) - KEEN, 1971: 667 (as syn. of *C. fergusonii*); fig. 1511 right (holotype).

Diagnosis: Coronations present only at very early stage, spire whorls slightly concave, aperture narrow; color yellow-orange, lighter color bands irregular, mottled; spire whorls mottled; spire color darker than that of body whorl.

Description: Shell medium-sized (maximum length 54 mm, with 10 teleoconch whorls); spire varying from low to moderately elevated; spire outline straight to somewhat concave; shoulder distinctly ridged, not coronated in mature stages; spire whorls flat to slightly concave, spire sculptured with faint growth lines and microscopic spiral striae; suture produced below the shoulder ridge, well defined but not deeply channeled; anal sinus of medium depth; body whorl profile with a faint convexity below the shoulder, basal profile variable from straight to convex or concave; surface smooth except for 10-15 spiral striae on base; aperture relatively narrow, of same width throughout and conforming to whorl profile. Protoconch homeostrophic, 3-whorled, smooth, light colored; shoulder of early teleoconch whorls coronated, coronations lost by 3rd to 6th teleoconch whorl; early juvenile shells with 2-3 in-

cised spiral striae below the shoulder. Color dark yellow to orange brown, with two irregular, often interrupted white bands; basal area variegated with white; white mottling at the shoulder produces light and dark radial markings on spire; ground color on spire of greater intensity than that of body whorl; aperture white within. Periostracum brownish, thin over body whorl, thicker on spire and produced in closely set, thin, arched ridges. Operculum bluntly unguiculate, about two times longer than wide.

Radula (Figure 3): Tooth of the "*Conus regularis* type" (NYBAKKEN, 1970), with single barb at the tip, a well-developed opposite blade extending about 1/3 the length of the tooth; serration prominent and extending about the same distance as the blade; waist slight; base enlarged with a small spur on one side.

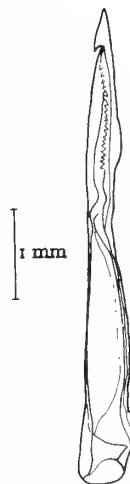


Figure 3

C. xanthicus, from 35.7 mm specimen (shell, Figure 21).
Radular tooth (scale = 0.1 mm)

Radula preparations were made from ten specimens, ranging in shell length from 14.2-54.3 mm, including those illustrated in Figures 13 (holotype), 15, 18, 19, 21, and 23. There was no significant variation in tooth morphology among the examined specimens.

Distribution and occurrence: Morro Colorado, Sonora, Mexico (type locality of *Conus chrysocestus*), to Rocas Octavia, Colombia (6°47'N; AHF 431-35); Revillagigedo Islands, Mexico, and Galápagos Islands, Ecuador. All oc-

currences are well offshore, chiefly in the 50-140 m depth range. We have examined 4 lots from Sonora, 14 lots from the southeastern side of Baja California from Isla Carmen to the Gorda Banks off Cape San Lucas, 12 lots from Isla Clarion, Revillagigedo Islands, 1 lot from southern Mexico, 1 lot from the Perlas Islands, Panama, 1 lot from Colombia (Figure 19) and 10 lots from the Galápagos Islands. The Rocas Octavia locality in Colombia is both the southernmost record known for *C. xanthicus* and the only station from which both *C. xanthicus* and *C. fergusonii* have been collected together.

Comparisons: Although *Conus xanthicus* could not be confused with large, fully mature specimens of *C. fergusonii*, it has been confused with immature specimens of the latter. Mature *C. xanthicus* differ from immature *C. fergusonii* in lacking coronations, producing the suture below (rather than at) the shoulder, having a narrower aperture, having an irregular, mottled (rather than even) banding pattern on the body whorl, and having a mottled (rather than unmarked) pattern on the spire. Juvenile *C. xanthicus* do not have the regular rows of spots of juvenile *C. fergusonii*. *Conus xanthicus* has a general resemblance to *C. virgatus* Reeve, 1849, but has a more angulate shoulder and does not have the axial color markings of that species. Like *C. fergusonii*, *C. virgatus* also produces the suture at the shoulder. Comparisons with *C. kohni* are given under the treatment of that species.

Variability: *Conus xanthicus* is highly variable in breadth and in spire profile. Too few specimens are available to fully document the range of variation, but some generalizations may be made. Those seen from Sonora are relatively low spired, although the spire of the holotype of *C. xanthicus* (Figure 13) is higher than that of the holotype of the synonymous *C. chrysocestus* (Figure 14). Those from the southeastern side of Baja California are similarly

variable, but some higher spired forms are known from the region (Figure 16). Specimens from Isla Clarion are rather small and uniform (Figure 18). The Colombian specimen (Figure 19) is rather narrow and high spired. Galapagan specimens (Figures 20-23) are rather uniformly narrow and moderately high spired.

Remarks: The holotype of *Conus xanthicus* (USNM 111236, Figure 13), from 130m off Guaymas, Sonora, Mexico, was not originally figured. The taxon was apparently not discussed again until HANNA & STRONG (1949) figured the holotypes and placed the name in the synonymy of *C. fergusonii*. The holotype of the synonymous *C. chrysocestus* Berry remains in the private collection of S. Stillman Berry, Redlands, California (Figure 14). It is also from Sonora, Mexico: "trawled in 30 to 45 fms., off Morro Colorado, Sonora; Antonio Luna, Dec. 1965." It is a large, brightly colored specimen which was not compared by Berry to *C. xanthicus*. He apparently did not question the long-held view of other authors concerning the validity of *C. xanthicus*.

Conus kohni McLean & Nybakken, spec. nov.

(Figures 4, 24-29)

Diagnosis: Coronations present only at very early stage, spire whorls markedly concave, aperture relatively broad; color yellow-orange, with mottled, lighter colored banding; spire with radial markings of same intensity as that of rest of shell.

Description: Shell medium-sized (maximum length 52.5 mm, with 9 teleoconch whorls); spire moderately elevated; spire outline slightly concave to straight; shoulder distinctly ridged, not coronated in mature specimens; spire whorls

Explanation of Figures 24 to 29

Conus kohni McLean & Nybakken, spec. nov.

- Figure 24: LACM 1885, holotype, 18-37 m, Isla Isabela, Galápagos Islands, Ecuador. Radula verified specimen, length 35.3 mm, periostracum removed ventrally, intact on spire.
- Figure 25: AHF 788-38, 101 m, coral & shell bottom, off Isla Daphne, Galápagos Islands, Ecuador. Length 52.3 mm, periostracum removed, lip broken back (largest specimen examined).
- Figure 26: AHF 788-38, same locality as Figure 25. Length 43.5 mm, periostracum intact.

- Figure 27: LACM 72-200, 40-45 m, coralline algal rubble, Bahía Academia, Isla Santa Cruz, Galapagos Islands, Ecuador. Radula verified specimen, length 40.0 mm, periostracum removed.
- Figure 28: CAS 46379, Isla Santa Cruz, Galápagos Islands, Ecuador. Length 33.6 mm, periostracum removed.
- Figure 29: AHF 324-35, 82 m, rock, Caleta Tagus, Isla Isabela, Galápagos Islands, Ecuador. Radula verified specimen, length 15.0 mm, periostracum partially intact (smallest specimen examined).



Figure 24

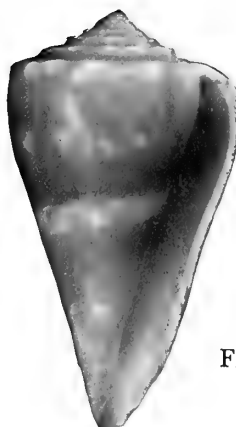


Figure 25

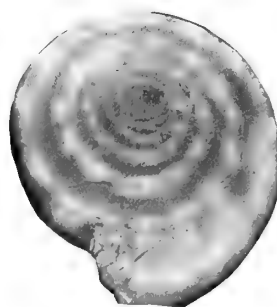


Figure 26



Figure 27

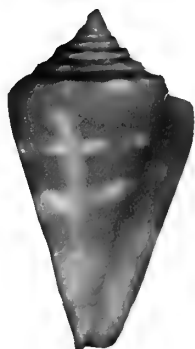
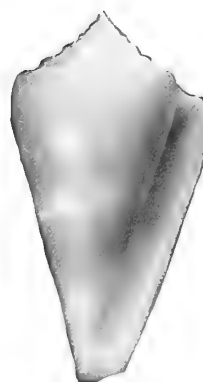
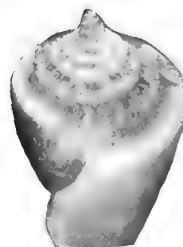


Figure 28



Figure 29



markedly concave, sculptured with faint growth lines; suture produced below the shoulder ridge, well defined but not deeply channeled; anal sinus of medium depth; outer lip thin, arcuate; body whorl profile with a convexity $1/8$ the distance below the shoulder and a slight concavity at $1/3$ the distance from the base; surface smooth except for 10-12 spiral lirae on the lower third of body whorl; aperture relatively wide, of same width throughout and conforming to the body whorl profile. Protoconch homeostrophic, 3-whorled, smooth, light colored; shoulder of first three teleoconch whorls weakly coronated, coronations lost by the 5th whorl. Color yellow to orange, with 2 more or less distinct spiral bands of white or less intense ground color, bands often narrow and bearing smaller white spots; the basal area may have some lighter mottling or less intense coloration; the shoulder bears another series of whitish spots that extend across the spire; ground color on the spire of equal intensity to that on the body whorl, aperture white within. Periostracum brownish, thin over body whorl, thicker on the spire and produced in closely set, thin, arched ridges. Operculum bluntly unguiculate, margins unserrated, about 3 times longer than wide. Dimensions of holotype: length 35.3 mm, width 18.7 mm, length of operculum 6.5 mm.

Radula (Figure 4): Tooth with 3 barbs, one near the tip and 2 on the opposite side; the first 2 barbs sharply pointed, the 3rd more rounded; serration lacking; the narrowest part of the tooth posterior to the 3rd barb and marked by a more or less abrupt step or shelf; posterior to the waist the shaft diameter expands to a maximum and then con-

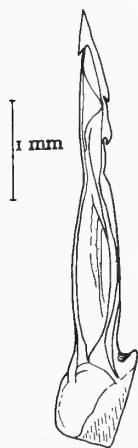


Figure 4

C. kohni, from 35.3 mm holotype specimen (shell: Figure 24)
Radular tooth (scale = 0.1 mm)

stricts slightly before the base; the base is large and bears a prominent spur.

Radula preparations were made from 6 specimens, including those illustrated in Figures 24 (holotype), 27, and 29. No variation was noted.

Type locality: 18-37 m, mud-silt bottom, Caleta Tagus, Isla Isabela, Galápagos Islands, Ecuador ($0^{\circ}24.5'S$, $90^{\circ}23'W$), 3 specimens collected by Gerald Wellington, 15 January 1975.

Type material: Holotype, LACM 1885; 1 paratype, CAS 59690; 1 paratype, USNM 758900.

Referred material (all Galápagos Islands, Ecuador): AHF 201-34, 46-64 m, Isla Espanola, 31 January 1934, 3 specimens; AHF 324-35, 82 m, Isla Isabela, 10 December 1934, 1 specimen; AHF 788-38, 101 m, Isla Daphne, 19 January 1938, 4 specimens; LACM 66-210, 34 m, Isla San Salvador, 24 September 1966, 1 specimen; CAS 46379, 100 m, Isla Santa Cruz, June 1969, 1 specimen; LACM 72-205, 40-45 m, Isla Santa Cruz, 31 January 1972, 3 specimens.

Distribution and occurrence: Galápagos Islands, Ecuador, on a variety of bottom types at depths of 18-100 m. At stations AHF 324-35 and 788-38 it occurred with *Conus xanthicus*. It may eventually be shown to occur elsewhere in the tropical eastern Pacific, although this now seems unlikely, considering that the region has been well sampled.

Etymology: We are pleased to name the species in honor of Dr. Alan J. Kohn of the University of Washington, who has contributed greatly to knowledge of the genus *Conus* over the past 20 years.

Comparisons: *Conus kohni* is similar to *C. xanthicus* in size and color pattern but may be distinguished on radula and shell characters. The radula tooth of *C. kohni* (Figure 4) differs from that of both *C. xanthicus* (Figure 3) and *C. fergusonii* (Figures 1, 2) in completely lacking a serration and having 3 barbs. The chief shell difference is the broader aperture of *C. kohni*, which increases the rate of expansion and results in mature shells of similar length having one less whorl. Mature shells typically have 10 whorls in *C. xanthicus* and 9 whorls in *C. kohni*. Additionally, shells of *C. kohni* are broader, the lower portion of the body whorl is more concave, the lip is more arcuate, and the spire whorls are more concave. The ground color and the color patterns are remarkably similar, although the lighter bands of *C. kohni* tend to be narrower. Comparison of specimens with the periostracum removed shows the ground color on the spire to be darker than the ground color of the body whorl in *C. xanthicus*, whereas in *C.*

kohni the ground color on the spire and on the body whorl is identical.

Variability: The 16 available specimens of *C. kohni* are uniform in proportions. Ground color varies from dark yellow to yellow-orange.

Remarks: Although specimens of *Conus kohni* were first collected over 40 years ago, the species has escaped notice until now, having no doubt been dismissed along with *C. xanthicus* as representative of the juvenile stage of *C. fergusonii*. Unlike *C. xanthicus*, however, misidentified specimens have not previously been illustrated. We were first alerted to its existence by discovery of an apparent discrepancy in radular characters among specimens thought to be *C. xanthicus*. Only after we had confirmed the presence of two species on radular characters were we able to recognize the associated shell characters that separate the 2 species.

Unfortunately we have not observed living examples of either *Conus xanthicus* or *C. kohni*, so we do not know if there are body color differences between the 2 species. Similarly we do not know if there are differences in habitat or bottom type preference. The bottom type data available for both species ranges from mud, sand, coral-line algal rubble, to rock, suggesting that both have a wide range of substrate occupancy.

DISCUSSION

Conus kohni is the only species of the genus at present considered endemic to the Galápagos Islands. Most mollusks known from the Galápagos Islands also occur in the tropical eastern Pacific, although there is a major endemic element and a small percentage of trans-Pacific migrants with Indo-Pacific faunal affinity.

Two Indo-Pacific species of *Conus* are known from the Galápagos: *Conus ebraeus* Linnaeus, 1758, and *C. chaldaeus* (Röding, 1798). These two species have also been reported from the mainland (see references in EMERSON, 1978). *Conus tessulatus* Born, 1778 is an Indo-Pacific species known from the Revillagigedo Islands and the mainland (EMERSON, 1978). It is possible that *C. kohni* is in this category, but if this is so, it remains to be discovered in the Indo-Pacific.

If *Conus kohni* is an eastern Pacific species, it may yet be found to occur elsewhere in the Panamic province, or it could represent a relict population surviving at the Galápagos Islands and extinct on the west American mainland. Few of the eastern Pacific Conidae, especially those that

occur offshore such as *C. xanthicus*, are known from the fossil record.

We have no data as to the food of *Conus fergusonii*, *C. xanthicus*, or *C. kohni*, but would anticipate that prey items would be different in all 3, based on major differences in tooth morphology. *Conus xanthicus* has a radula tooth morphology that is the most common in the genus, a type that NYBAKKEN (1970) termed "regularis." At least nine other Panamic species have a similar tooth (NYBAKKEN, *op. cit.*). The food of these species, where known, consists of errant polychaetes (NYBAKKEN, 1979). *Conus fergusonii* has a radula tooth similar to that of *C. princeps* Linnaeus, 1758, and *C. patricius* Hinds, 1843. Again, errant polychaetes should be the preferred food for species with a similar tooth (Nybakken, in press). The tooth of *C. kohni* is of an uncommon type for which no food data are available for any species with a similar morphology. It is most similar to that of the eastern Pacific species *C. recurvus* Broderip, 1833, and *C. arcuatus* Broderip & Sowerby, 1829.

The similarity between the tooth of *Conus kohni* and *C. recurvus* leads us to compare the shell morphology of the 2: proportions are similar; both have the concave shoulder and a markedly arcuate lip, but a very different color pattern. If other evidence can be found to support the theory that *C. kohni* and *C. recurvus* are closely related, it will imply that the similarity of color pattern between *C. xanthicus* and *C. kohni* is coincidental and convergent and that tooth structure is a conservative character. An alternative possibility is that the similar color pattern of *C. kohni* and *C. xanthicus* is the conservative feature and that the tooth structure has diverged in response to changes in diet.

Small specimens of *C. fergusonii* evidently have a different radula tooth morphology from that of large specimens. The tooth of a 26.0 mm long specimen is shown in Figure 1. The next smallest specimen from which we have obtained a radula is 43.5 mm in length. Its tooth, as in others from shells of larger sizes we have prepared (shell lengths, 85.1, 61.0, 60.7, and 51.9 mm) is similar to that of Figure 2. The tooth of the smallest specimen is proportionately shorter, lacks the second barb and has the first barb very weakly developed. The fact that the serration is the same, running half the length of the tooth, enables us to consider the transition to be reasonable, in the absence of intermediate-sized examples.

This is the second known species of *Conus* in which a change in radular tooth morphology has been demonstrated. NYBAKKEN (1970: 13) found that the radula tooth of a specimen of *C. patricius* 27.1 mm in length was

proportionately shorter than that of the adult and entirely lacked the blade, barb, and serration. That, however, probably represented an earlier stage of tooth development than in our example with *C. fergusoni*. NYBAKKEN (1970) found that other *Conus* species examined did not show any significant change in tooth morphology between young and mature specimens. Both species reach large sizes — changes in tooth morphology with growth may prove to be a feature of only those species that attain the largest sizes.

In addition to large size and similar tooth morphology, both *Conus fergusoni* and *C. patricius* have coronations in immature stages that are not formed in fully mature stages. The subgenus *Pyriconus* Olsson, 1967, was proposed for *C. patricius* (type species) and fossil species with a similar pyriform shape (OLSSON, 1967: 21). Although *C. fergusoni* is not similarly pyriform, it is evidently related and may also be tentatively assigned to the subgenus. However it is premature to attempt assignment of the other species treated here.

CONCLUSIONS

Two of the 3 possible explanations originally suggested by NYBAKKEN (1970) to account for different radula tooth morphologies in the then understood *Conus fergusoni* have proven to be the case: 2 species were being confused, and tooth morphology in *C. fergusoni* does change with growth. Change of tooth morphology with growth is evidently unusual in the genus and its occurrence in other species should be further documented.

Recognition of *Conus xanthicus* has long been delayed because of confusion with immature specimens of *C. fergusoni*, due no doubt to the rarity of the earliest stages of *C. fergusoni* — for reasons not apparent. Previous authors had not realized that coronated early whorls are a feature of *C. fergusoni* and that small specimens have spiral rows of dark spots. *Conus fergusoni* is not highly variable, whereas *C. xanthicus* is unusually variable in elevation of the spire.

Conus xanthicus and the herein described *C. kohni* have been confused because of a nearly identical color pattern. The two may be separated on radula and shell characters. It remains to be demonstrated whether they are closely related or are more nearly related to other species having corresponding tooth morphologies.

Despite a spate of recent papers on the systematics of Eastern Pacific *Conus*, none of these papers contain rigorous comparative diagnoses of the shells, nor do we have information about the color of living animals or food habits for many of the species. Progress has been made

with documentation of tooth morphologies. Future systematic work on the genus should include a discussion of radula characters.

NOTE ADDED IN PROOF

After this paper was submitted, we received "Cone Shells: A Synopsis of the Living Conidae," by Jerry G. Walls, 1011 pages, T. F. H. Publications, Inc., Neptune, N.J., published March 6, 1979. Our conclusions about the validity of *Conus xanthicus*, the synonymy of *C. chrysocestus*, and the spotted juveniles of *C. fergusoni* were also reached by Walls. However, he included *C. fulvocinctus* Crosse, 1873, in the synonymy of *C. fergusoni*, an opinion not shared by us. The locality for *C. fulvocinctus* was originally given as West Africa, and the 75 mm long specimen was said to have a thin periostracum. The original figure shows strong spiral cords extending from the base to the mid-whorl, spire whorls that are convex rather than concave, and no trace of coronations in early stages. We agree, however, that *C. consanguineus* E. A. Smith, 1880, locality unknown, is a probable junior synonym of *C. fergusoni*.

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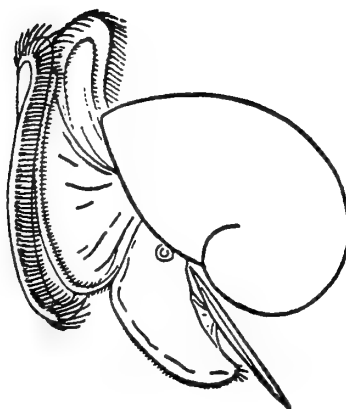
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The Family Lepidopleuridae

(Mollusca : Polyplacophora)

in the Eastern Pacific

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(4 Plates; 8 Text figures)

INTRODUCTION

THE TAXONOMY of the eastern Pacific lepidopleurids has long remained uncertain. These most primitive of Recent chitons are usually small in size, uniform in color, fragile, and scarce in numbers. They do not lend themselves easily to study given the simplicity of their anatomical features. In museum collections they are represented by few and small lots, which makes it difficult to draw firm conclusions about intraspecific variations and interspecific distinctions.

The family Lepidopleuridae has never been reviewed. In the eastern Pacific, chiton workers have often suspected that far too many nominal species (Dall alone named 13) of lepidopleurids had been described. Insufficiently characterized, unfigured, known only from the type material (often limited to 1 or 2 specimens), many such nominal species of eastern Pacific lepidopleurids have crowded the chiton nomenclature in the long wait for a taxonomic decision about their validity.

It is the purpose of this paper to review the lepidopleurids of the eastern Pacific, and, following the study-plan of the late ALLYN G. SMITH (1977), to contribute to the rectification of the west coast chiton nomenclature.

The present work draws mostly upon material in the collections of the California Academy of Sciences (CAS), Stanford University (SU) [at CAS], Natural History Museum of Los Angeles County (LACM), San Diego Museum of Natural History (SDNH), and Academy of Natural Sciences

of Philadelphia (ANSP). However, particular emphasis must be given to the contributions of Dr. Joseph Rosewater who graciously permitted me to examine and study critical type material in the repository of the National Museum of Natural History (USNM), and of Piet Kaas (The Netherlands), Richard Van Belle (Belgium), and Dr. B. Sirenko (Leningrad, U.S.S.R.) who generously provided me with valuable specimens and data.

This review of the family Lepidopleuridae is limited to the area known as eastern Pacific, which extends from the Bering Strait (65.5° N) to the northern tip of Chiloé Island, Chile (44° S), through the north cold temperate, north warm temperate, tropical, and south warm temperate regions of the west coast of the Americas. It excludes the poorly known (to the author) south cold temperate region (Magellanic Province) which starts at Chiloé Island. From this investigation 7 species are recognized as components of the lepidopleurid fauna of the eastern Pacific:

Leptochiton rugatus (Pilsbry, 1892)

Leptochiton nexus Carpenter, 1864

Leptochiton alveolus (Lovén, 1846)

Leptochiton incongruus (Dall, 1908)

Leptochiton albemarlensis Smith & Ferreira, 1977

Hanleyella oldroydi (Dall, 1919)

Oldroydia percrassa (Dall, 1894)

The following descriptions and synonymies of species are not intended to be exhaustive. Repetition of what is already easily available in the literature is avoided in favor of extending the descriptions and differential diagnoses of the species involved.

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SYSTEMATIC TREATMENT

POLYPLACOPHORA de Blainville, 1816

Neoloricata Bergenhayn, 1955

LEPIDOPLEURINA Thiele, 1910

LEPIDOPLEURIDAE Pilsbry, 1892

Definition: "Relatively small [less than 5 cm long]; valves generally sculptured with granules set in lines or quincunx; valve coverage complete; girdle narrow, minutely spiculate or scaly [or both]; insertion plates lacking, or if present, weak and unslit; articulamentum layer usually consisting only of weakly developed sutural laminae in valves ii to viii. Gills short, posterior." (SMITH, 1960b: 52).

Type-genus: *Lepidopleurus* RISSO, 1826 [not DALL, 1879] (Type species: *Chiton cajetanus* POLI, 1791, by SD, HERMANNSEN, 1847).

Leptochiton Gray, 1847

Definition: Valves rounded and thin. Tegmental surface with granules in lines or quincunx. Lateral areas low and inconspicuous. Girdle narrow, with minute scales or scale-like processes, often with interspersed small spines.

Type Species: *Chiton cinereus* MONTAGU, 1803 (not *Chiton cinereus* LINNAEUS, 1767) [= *Chiton asellus* Gmelin, 1791] by SD, GRAY (1847, Nov.).

Synonyms:

Terenochiton Iredale, 1914b [type species, *Lepidopleurus* (*Terenochiton*) *subtropicalis* Iredale, 1914, by OD]; *Xiphiozona* BERRY (1919a) [type species, *Lepidopleurus* (*Xiphiozona*) *heathi* BERRY, 1919, by OD].

Remarks: GRAY (1847a) defined *Leptochiton* on the basis of the "valves rounded and thin" which clearly distinguished its type species, *Chiton cinereus* MONTAGU, 1803, from *Chiton cajetanus* POLI, type species of *Lepidopleurus* RISSO, 1826. By citing *C. cinereus* together with *C. cajetanus* GRAY introduced an element of uncertainty as to the validity of *Leptochiton*; however, this uncertainty was dispelled when GRAY (1847b) listed *C. cinereus* as type of *Leptochiton* GRAY, and *C. cajetanus* as type of *Lepidopleurus* RISSO.

DALL (1879b) accepted *Leptochiton*, but PILSBRY (1892) placed it in the synonymy of *Lepidopleurus*. IREDALE, having at first recognized *Leptochiton* (1914a), erected a

new genus, *Terenochiton*, for "the small Australian '*Lepidopleurus*'" which have "nothing in common save the absence of insertion plates" with the type of *Lepidopleurus* (IREDALE, 1914b: 29). BERRY (1917) rehabilitated GRAY's *Leptochiton* pointing out that "the relatively delicate and smooth shelled *Lepidopleuridae* of the west American coast seem only diffidently congeneric with *L. cajetanus* POLI, the thick rugose shell selected by PILSBRY as RISSO's type." And although introducing *Xiphiozona* (1919a), BERRY decided "to retain" *Leptochiton* (1919b: 6, footnote) as the proper generic name to be used for most west American *lepidopleurids*.

ALLYN G. SMITH at first (1960a) considered *Leptochiton* as a subgenus of *Lepidopleurus*; but in the Treatise (1960b) SMITH regarded *Leptochiton* as a synonym of *Lepidopleurus* RISSO. However, in an unpublished revision of the chiton classification, on file at CASG, SMITH had reaccepted *Leptochiton* and conferred it generic rank. In the most recent classification of Polyplacophora, VAN BELLE (1975) also accepted *Leptochiton*, although treating it as a subgenus of *Lepidopleurus*.

Terenochiton Iredale, 1914, was placed in the synonymy of *Leptochiton* by SMITH (1960b), and VAN BELLE (1975). The examination of 66 specimens of *Terenochiton inquina-tus* (REEVE, 1847), collected in 9 localities on the east coast of North Island, New Zealand (AJF 382-385, 387-391) demonstrated that in all respects of shell, girdle, and radula, the species belongs quite properly in the genus *Leptochiton*.

Leptochiton GRAY is here given full generic rank in the recognition of GRAY's original description, and the uniformity of characteristics typified in *Leptochiton asellus* (Gmelin, 1791).

Leptochiton rugatus (Pilsbry, 1892)

(Figures 1, 2, 7, 33, and 34)

Leptochiton internexus rugatus DALL, 1879b: 319 (nomen nudum)

Lepidopleurus rugatus PILSBRY, 1892: 11-12; pl. 3, figs. 67-70. 1898: 287 - BERRY, 1907: 47 - CHACE, 1917: 44 - DALL, 1921: 186 (in section *Leptochiton*) - OLDROYD, 1927: 849 (in section *Leptochiton*) - BURCH, 1942: 7 - CHACE, 1958: 330 - ABBOTT, 1974: 393

Leptochiton rugatus (Pilsbry). THIELE, 1909: 12-13; pl. 1, figs. 41-50 - SMITH, 1947a: 6. 1947b: 17 - SMITH & GORDON, 1948: 205 - PALMER, 1958: 263; pl. 28, fig. 7; pl. 35, fig. 3 - LINDSAY, 1966: 348 - BURGHARDT & BURGHARDT, 1969: 26; pl. 2, fig. 35 - THORPE in KEEN, 1971: 863; Polyplacophora, fig. 1 - A. G. SMITH in R. I. SMITH & CARLSON, eds. (Light's Manual, 3rd ed.), 1975: 262, 265.

Leptochiton internexus DALL, 1879b: 319 (nomen nudum)

Lepidopleurus internexus CARPENTER in PILSBRY, 1892: 12 – DALL, 1921: 186 (in section *Leptochiton*) – OLDROYD, 1927: 849 (in section *Leptochiton*) – LA ROCQUE, 1953: 8 – BURGHARDT & BURGHARDT, 1969: 24; plt. 2, fig. 34 – ABBOTT, 1974: 393

Leptochiton internexus (Carpenter in Pilsbry). SMITH 1947a: 4. 1947b: 17 – PALMER, 1958: 262, plt. 28, figs. 3-6

Leptochiton cancellatus (Sowerby). DALL, 1879b: 315-317. 1886: 211 – BERRY, 1917: 232-233 – WILLETT, 1919: 27 – BERRY, 1927: 160 – SMITH, 1947a: 4. 1947b: 17 – SMITH & GORDON, 1948: 205 – BERRY, 1951: 218. [not *Chiton cancellatus* Sowerby, 1839]

Lepidopleurus cancellatus (Sowerby). PILSBRY, 1892: 3-5 (in part) – DALL, 1921: 186 – OLDROYD, 1924: 184. 1927: 848-849 – LÉLOUP, 1940: 6-7; figs. 10-11, 16-18 – BURCH, 1942: 7 – BURCH & BURCH, 1943: 5 – JAKOVLEVA, 1952: 46-47; fig. 14; plt. 1, fig. 2 (in part) – LA ROCQUE, 1953: 7 (in part) – TAKI, 1964: 407 – ABBOTT, 1974: 392 (in part). [not *Chiton cancellatus* Sowerby, 1839]

Lepidopleurus assimilis THIELE, 1909: 11-12, plt. 1, figs. 30-39 – TAKI & TAKI, 1929: 162 – TAKI, 1938: 328-331; plt. 14, fig. 2; plt. 16, figs. 5, 9-13, 15; plt. 17, figs. 9-11 – JAKOVLEVA, 1952: 48-49; fig. 16; plt. 1, fig. 4 – TAKI, 1962: 31 – TAKI, 1964: 408

Lepidopleurus alascensis THIELE, 1909: 13; plt. 1, figs. 51-60 – DALL, 1921: 187 – (in section *Leptochiton*) – ABBOTT, 1974: 393

Leptochiton alascensis (Thiele). SMITH, 1947a: 3. 1947b: 17

Type Material:

Leptochiton rugatus (Pilsbry, 1892): Syntypes (ANSP 35586) ["two whole specimens plus completely disarticulated valves without girdle," M. Miller, *in litt.*, 27 March 1978].

Lepidopleurus internexus Carpenter in Pilsbry, 1892: Holotype (USNM 30750); two accompanying labels give locality as "Sta. Barbara," California.

Lepidopleurus assimilis Thiele, 1909: Types at the Zoologisches Museum, Humboldt Universität, Berlin ["1 set of plates (a little dilapidated), locality Sachalin (it must be the holotype), and 1 dried specimen, locality Wladiwostok (marked as a type)" Dr. R. Kilias, *in litt.*, 6 September 1978].

Lepidopleurus alascensis Thiele, 1909: Holotype at Zoologisches Museum, Humboldt Universität, Berlin ["(in alcohol), locality Alaska," Dr. R. Kilias, *in litt.*, 6 September 1978].

Type Locality: "near S. Tomas River, Lower California," Mexico [$31^{\circ}32'N$; $116^{\circ}26'W$], as indicated in the label accompanying the syntypes [M. Miller, *in litt.*, 27 March 1978].

Description: The original description of PILSBRY (1892), supplemented in THIELE (1909), is very adequate to identify the species. Color, a uniform creamy white; some specimens may be orange color as described for "*internexus*" by CARPENTER in PILSBRY (1892), and often seen in "*assimilis*" from Japan; and some may be blackened by fuliginous material. In size, specimens from Alaska tend to be appreciably smaller than those from the southern part of the range;

largest specimen examined measures 15.8 mm in length, including girdle (LACM 62-8: "Intertidal, Franklin Point, San Mateo County, California, leg. J. H. McLean, June 1962-November, 1963"). Based on 10 adult specimens, the width/length ratio is 0.53. Specimens of *Leptochiton rugatus* are somewhat variable in height; however, a constant diagnostic feature is the definitely rounded, i.e., not carinated, back (Figure 1). Tegmental sculpture consists of microgranules linearly juxtaposed to form subgranose riblets (Figure 2). These riblets are longitudinally disposed in the central areas (about 20-40 riblets per side), somewhat radially oriented in the end valves and lateral areas (about 10-15 per area). The strength of these sculptural features is quite variable, as is the degree of crowding of the riblets and their microgranulose appearance; the space between the riblets may appear, at first glance, pitted or cancellate.

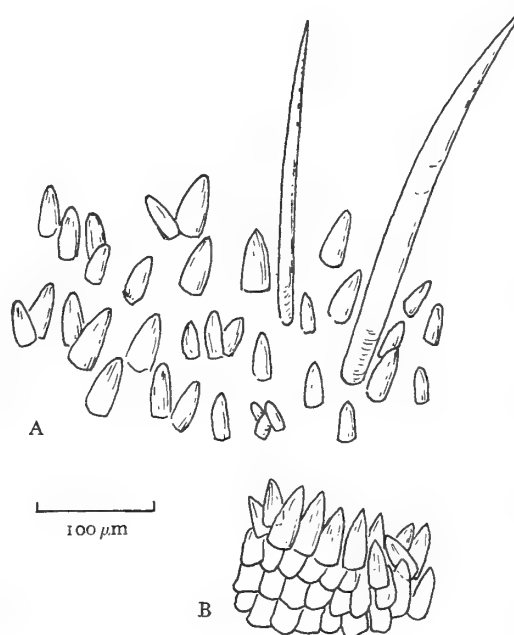


Figure 33

Leptochiton rugatus (Pilsbry, 1892)

Girdle scales and spines of (A) the upper surface, and (B) the under surface. Specimen collected at Monterey Bay, California at a depth of 8 m (AJF 50)

Mucro, central to subcentral, often a bit pointed and elevated; postmucro, quite variable, convex to concave, often dropping abruptly. Lateral areas of intermediate valves usually inconspicuous; in many specimens they show con-

centric, more or less coarse and irregular growth lines. Girdle, pebbly to gravelly in appearance, with no conspicuous spicules or spines; in some specimens there may be a definitely spiculous appearance at the sutures. Girdle scales (Figure 33), mostly conical, irregularly striated, small (about 60-80 μm in height, 20-40 μm in diameter of base), close together but not imbricated. An occasional scale is elongated to the point it could be called a spinule, a feature more often seen at the sutures where, in some specimens, they form small ill-defined tufts. Girdle undersurface covered with small triangular scales, about 40 μm x 20 μm , imbricated, pointing outward. Girdle scales display considerable degree of polymorphism in size and shape, not seemingly related to locality or depth.

The radula of *Leptochiton rugatus* was first described by THIELE (1909). Consistently, in the specimens examined, it comprised over 100 rows (170 in 1 specimen) of mature teeth. A specimen (AJF 50: Monterey Bay, California, at 8 m depth), measuring 10.3 mm in length, has a radula 3.9 mm long (i.e., 37% of the specimen's length), with 146 rows of mature teeth. The central tooth (Figure 34) has a relatively narrow front end, about 18 μm in width, with a small

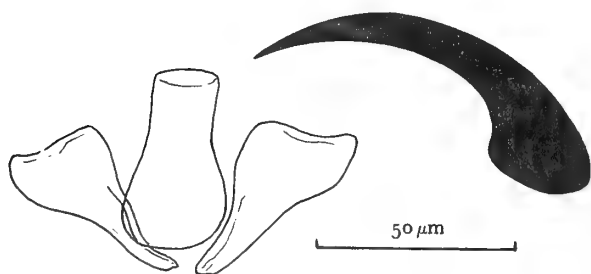


Figure 34

Leptochiton rugatus (Pilsbry, 1892)

Radula: Median, first lateral and head of second lateral tooth. Specimen collected at Monterey Bay, California at a depth of 8 m (AJF 50)

blade. First lateral teeth, aliform, wider in the front. Major lateral teeth with a very long (90 μm), unicuspid head. Outer marginal teeth about 22 μm in length, and 44 μm in width; length/width ratio, 0.5. The examination of the radula of several specimens from different localities, from Alaska to Baja California and the Gulf of California, disclosed no appreciable variation or discrepancy in these essential characteristics. A specimen of "*assimilis*" from Vostock Bay, Sea of Japan (collected by B. Sirenko, July 26, 1971, at a depth of 5 m), generously donated by Dr. B. Sirenko, Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R., measuring 5.2 mm in length, has a radula 3.3 mm long (53% of shell length) with about 170 rows of mature teeth; the median tooth is narrow in front where it measures 13 μm in width; major lateral teeth have very long (45 μm), unicuspid heads; outer marginal teeth are 20 μm in length, 38 μm in width (length/width ratio, 0.52). These observations, in the absence of significant conchological distinctions, are to be regarded as well within the expected variation in *L. rugatus*, particularly when differences in geographical sites are considered.

Distribution: *Leptochiton rugatus* has a seemingly continuous distribution from Alaska to Magdalena Bay, Baja California, Mexico. The northernmost verified record is Cohen Island, Kachemak Bay, Kenai Peninsula, Alaska (59°32.5' N; 151°28.5' W), leg. J. H. McLean & R. Baxter, July 31, 1973 (LACM 73-20); the southernmost record is at Magdalena Bay, "about 1 mile northeast of Pta. Belcher," Baja California, Mexico (24°35' N; 112°05' W), leg. J. H. McLean & Oringer, Dwyer Expedition, December 14, 1967 (LACM 67-70). *Leptochiton rugatus* has been collected in the Aleutian Islands (CASG 39538), and in the offshore islands: Heskett (LACM 73-23), Kodiak (LACM 75-32), Queen Charlotte (LACM 66-46; LACM 70-95), Vancouver (LACM A.4052; LACM-AHF 1151-40; LACM 63-62; LACM 66-36; LACM 73-40), Orcas (LACM M-541; LACM M-544), Farallon (LACM 62-9), Anacapa (LACM-AHF 874-38), Santa Rosa (LACM-AHF 1385-41; LACM 73-10), Santa Cruz (LACM-AHF 1192-40; LACM-

Explanation of Figures 1 to 8

Figure 1: *Leptochiton rugatus* (Pilsbry, 1892). 12.3 mm long. Monterey, California (LACM 59-12)

Figure 2: Close-up of specimen in Figure 1 to show detail of central and lateral areas

Figure 3: *Lepidopleurus nexus* Carpenter, 1864. Holotype (USNM 16270)

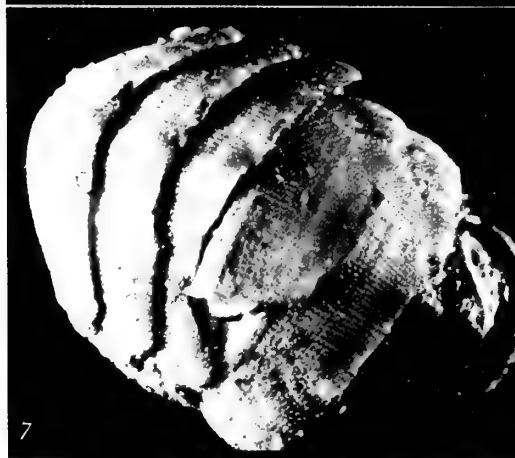
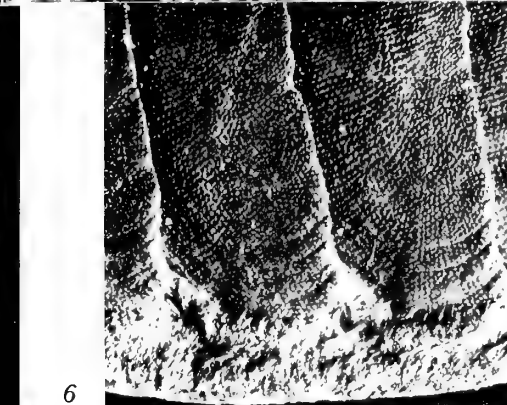
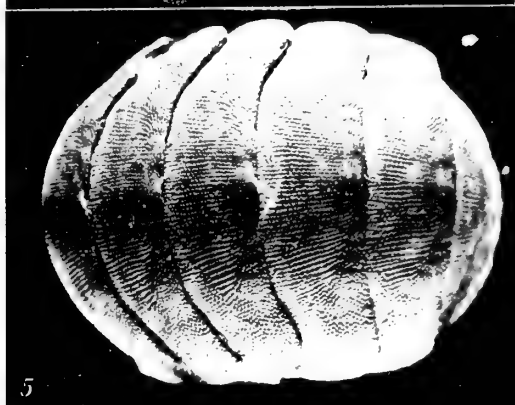
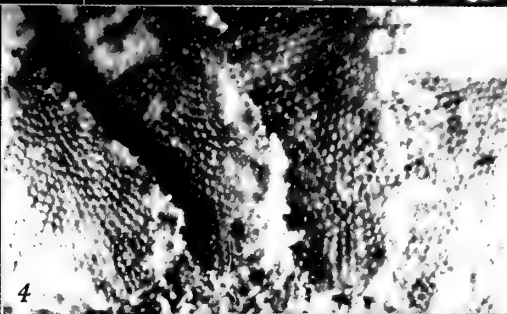
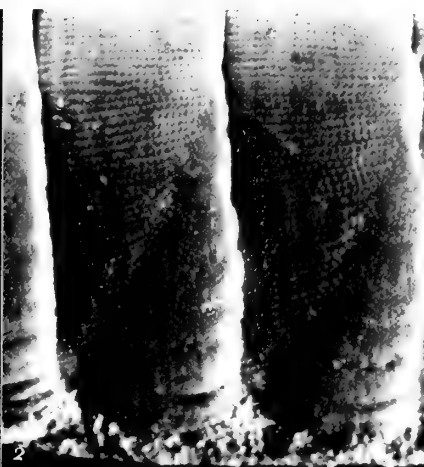
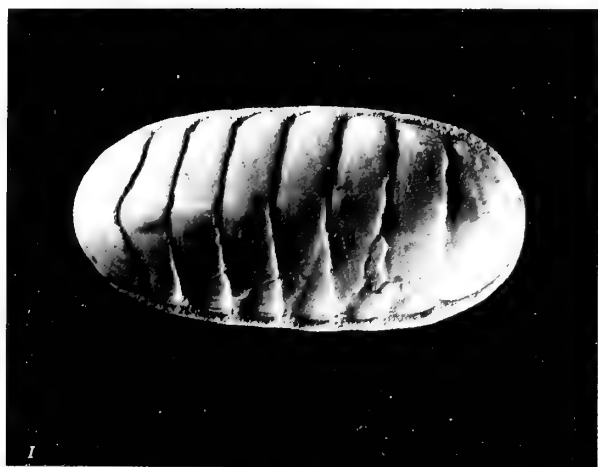
Figure 4: Close-up of specimen in Figure 3 to show detail of central and lateral areas

Figure 5: *Lepidopleurus ambustus* Dall, 1919. Paralectotype (herein designated) (USNM 274120)

Figure 6: *Lepidopleurus ambustus* Dall, 1919. Lectotype (herein designated): Close-up of the lectotype to show detail of central area, lateral areas, and girdle (USNM 274120)

Figure 7: *Lepidopleurus internexus* Carpenter in Pilsbry, 1892. Holotype (USNM 30750)

Figure 8: *Lepidopleurus lycurgus* Dall, 1919. Holotype (USNM 274119)



AHF 1196-40), Catalina (LACM-AHF 1149-40; LACM-AHF 1151-40; LACM-AHF 1323-41; LACM-AHF 1430-41; LACM 65-6), and Guadalupe (LACM-AHF 1924-49). In what may be an isolated population, *L. rugatus* is also present throughout most of the Gulf of California, from "Puertecitos to Bahía de los Angeles, Baja California, and in the Guaymas region of Sonora, Mexico" (THORPE in KEEN, 1971), as verified by specimens collected at Puertecitos (LACM 62-19), Bahía de San Francisquito (AJF 36), and San Augustine, Sonora (AJF, August, 1972).

Leptochiton rugatus, identified as "*assimilis*" and "*cancellatus*," has been reported off the coasts of U.S.S.R., Sea of Japan, Sea of Okhotsk, and the Bering Sea.

Bathymetrically, *Leptochiton rugatus* ranges from the intertidal zone to 458 m (LACM 1058, off Catalina Island, California). Median depth, based on the lots examined, 14 m.

Remarks: As reflected in the literature and museum labels, many serious students of chitons have held the view that the "*rugatus*"-like specimens of the eastern Pacific represent two or more distinct species. However, the observations made in the course of this study indicate that, at least on conchological grounds, all specimens examined should be regarded as conspecific. Radula studies did not contradict this first impression.

But the question remained whether the eastern Pacific species, *Leptochiton rugatus* (Pilsbry, 1892) was conspecific with *L. cancellatus* (Sowerby, 1839) from the North Atlantic. From the original descriptions of *L. rugatus* and *L. cancellatus* it seemed impossible to differentiate the two populations, Pacific and Atlantic, with certainty. Fortunately, thanks to the generous assistance of Richard A. Van Belle, Sint-Niklaas, Belgium, who provided several specimens of *L. cancellatus* collected at Trébeurden, Bretagne, France, and at Kostenäuman, Sweden, it was possible to compare directly eastern Pacific with Atlantic specimens.

Side by side, eastern Pacific specimens of *L. rugatus* appeared to be conchologically indistinguishable from the Atlantic *L. cancellatus* in size, color, shape, tegmental sculpture and articulation; and although the Atlantic specimens seemed to have a slightly higher and rounder back, and a lesser tendency to have spinule-like girdle elements than their Pacific counterparts, the differences were trivial and short of specific significance.

There were, however, appreciable differences in the radulae. Comparing the radulae of 10 specimens of *Leptochiton rugatus* from different localities in the eastern Pacific with those of 3 specimens of the Atlantic *L. cancellatus* it was observed that the radula of the eastern Pacific specimens consistently had (1) considerably more rows of

mature teeth (> 100 rows in *L. rugatus* vs. 50-70 rows in *L. cancellatus*), (2) a differently shaped median tooth (anterior end much narrower than posterior end in *L. rugatus* vs. anterior end as wide or wider than posterior end in *L. cancellatus*), (3) major lateral teeth with a distinctly different head (unicuspid, very long and slender in *L. rugatus* vs. bicuspid, relatively short and thick in *L. cancellatus*), and (4) outer marginal teeth much shorter than wide (length/width ratio about 0.5) in *L. rugatus* but longer than wide (length/width ratio 1.2 to 1.6) in *L. cancellatus*. In view of these marked radular differences, it is concluded that the 2 populations, Atlantic and Pacific, despite their very great conchological similarities, represent 2 different species, with the eastern Pacific species taking the name proposed by PILSBRY (1892), *L. rugatus*. *Leptochiton cancellatus* (Sowerby, 1839) is not present in the Pacific collections examined.

The synonymies of *Leptochiton assimilis* Thiele, 1909, and *L. alascensis* Thiele, 1909 are based on the original description and figures of the species; the examination of several specimens of *L. assimilis* collected at the Okhotsk Sea and Sea of Japan, and generously donated by Drs. Golikov and B. Sirenko, Zoological Institute, Academy of Sciences, Leningrad, U. S. S. R., demonstrated their conspecificity with *L. rugatus*.

Leptochiton internexus (Carpenter in Pilsbry, 1892) is here regarded as a synonym of *L. rugatus*, on the basis of the original description as well as on the direct examination of the holotype (USNM 30750), available through the courtesy of Dr. Joseph Rosewater. The single type specimen (Figure 7), dry, has a light brown color; valves i, vii, and viii are disarticulated. In every respect, it corresponds to *L. rugatus*. Color slides of the holotype are deposited in the California Academy of Sciences Invertebrate Zoology (CASIZ), Color Slides Series. The conspecificity of *L. internexus* was further confirmed through the study of a lot of 40 specimens so labelled probably on account of its locality and beautiful orange-gold color of the shells (LACM 63-69, 8 km SE of Point Conception, Santa Barbara County, California, at 13-17 m, under kelp, leg. J. H. McLean, July 18-19, 1963). There were no significant differences in shell, girdle, and radula, between these specimens and those of other populations of *L. rugatus*.

Leptochiton nexus Carpenter, 1864

(Figures 3 to 6, 8, 35, and 36)

Leptochiton nexus CARPENTER, 1864: 612 (*nomen nudum*), 650 [Reprinted, 1872: 98, 136]. 1866: 212-213. COOPER, 1867: 23 - DALL, 1879b: 319 - LOWE, 1904: 19 - SMITH, 1947a: 6. 1947b: 17 - SMITH & GORDON, 1948:

- 205 - PALMER, 1958: 262; plt. 28, fig. 2 - BURGHARDT & BURGHARDT, 1969: 25
- Lepidopleurus nexus* (Carpenter). PILSBRY, 1892, 14: 11. 1898: 287 - OLDROYD, 1911: 74 - DALL, 1921: 187 (in section *Xiphiozona*) - OLDROYD, 1927: 853 (in section *Xiphiozona*) - WILLETT, 1935: 42 (with syn. *L. heathi* Berry, 1919, and *L. ambustus* Dall, 1919 - BURCH, 1942: 7 - BURCH & BURCH, 1943: 5 - ABBOTT, 1974: 393
- Chiton (Leptochiton) nexus* (Carpenter). ORCUTT, 1885: 544
- Lepidopleurus (Xiphiozona) heathi* BERRY, 1919a: 5 - HANSELMAN, 1977: 62
- Lepidopleurus heathi* (Berry). DALL, 1921: 187 (in section *Xiphiozona*) - OLDROYD, 1927: 853 (in section *Xiphiozona*) - WILLETT, 1935: 42 (syn. of *L. nexus*)
- Leptochiton (Xiphiozona) heathi* (Berry). BERRY, 1919b: 6-8; plt. 1, figs. 1-2; plt. 2
- Leptochiton heathi* (Berry). SMITH, 1947a: 4. 1947b: 17 - SMITH & GORDON, 1948: 205 - BURGHARDT & BURGHARDT, 1969: plt. 2, fig. 33 (with syn. *L. ambustus* Dall, 1919)
- Lepidopleurus ambustus* BERRY, 1907: 47 (*nomen nudum*)
- Lepidopleurus (Leptochiton) ambustus* DALL, 1919: 499-500
- Lepidopleurus ambustus* Dall. DALL, 1921: 187 (in section *Leptochiton*) - OLDROYD, 1927: 849-850 (in section *Leptochiton*) - WILLETT, 1935: 42 (syn. of *L. nexus*)
- Lepidopleurus (Pilsbryella) ambustus* Dall. LELoup, 1940: 4-6, figs. 1-7
- Leptochiton ambustus* (Dall). SMITH, 1947a: 3-4. 1947b: 17 - SMITH & GORDON, 1948: 205 - BURGHARDT & BURGHARDT, 1969: 24 (syn. of *L. heathi*).
- Lepidopleurus (Leptochiton) lycurgus* DALL, 1919: 500
- Lepidopleurus lycurgus* Dall. DALL, 1921: 187 (in section *Leptochiton*) - OLDROYD, 1927: 850 (in section *Leptochiton*) - ABBOTT, 1974: 393
- Leptochiton lycurgus* (Dall). SMITH, 1947a: 4. 1947b: 17 - BURGHARDT & BURGHARDT, 1969: 25

Type Material:

Leptochiton nexus Carpenter, 1864. Holotype (USNM 16270)

Leptochiton (Xiphiozona) heathi Berry, 1919. Holotype (S.S. Berry colln., Cat. No. 3513), "off Monterey, California." Not examined.

Lepidopleurus ambustus Dall, 1919: Lectotype [herein] and 2 paralectotypes (USNM 274120); accompanying label gives locality as "Sta Barbara Chan./Sta. Barbara Ids.," California.

Lepidopleurus (Leptochiton) lycurgus Dall, 1919: Holotype (USNM 274119); accompanying label reads "Catalina Id."

Type Locality: Catalina Island, Los Angeles County, California [33°23'N; 118°24'W].

Description: Carpenter's original description in the "Guide to the Diagnosis of the Vancouver and California Shells" (1864: 650) is far from adequate: "236. *Leptochiton nexus*, n.s. Like *asellus*: scarcely sculptured: mantle-margin with striated chaffy scales, like *Magdalenensis*, interspersed with transparent needles. 20-80 fm. *Cp.*" The species is not figured; in a table on the same p.650, it is indi-

cated that the specimen(s) was collected in the islands of the Sta. Barbara Group, by Cooper.

Seemingly quoting from Carpenter's unpublished manuscript, PILSBRY (1892, 14: 11) enlarged upon this description: "Shell small, whitish-ashen, valves gothic-arched; lateral areas scarcely defined; entire surface ornamented with series of subquadrate granules, the series longitudinal upon the central, radiating upon the lateral areas and end valves, very close, scarcely interrupted. Jugum elevated, subacute; umbones inconspicuous. Mucro conspicuous, median. Inside with strong sutural lobes and a wide plane sinus to the middle valves; insertion plates obsolete. Girdle having a narrow, close, striated scales and needle-shaped, crystalline bristles here and there and around the margin. (*Cpr.*)" To which Pilsbry added, later on the page: "A variety is prettily variegated with olive, has stronger sculpture, and the valves slightly beaked. The spicules which appear on the girdle among the striated, elongated scales, are very numerous. It is curiously like the young of *Ischnochiton radians*. (*Cpr.*)" The species was left unfigured until PALMER (1958, plt. 28, fig. 2).

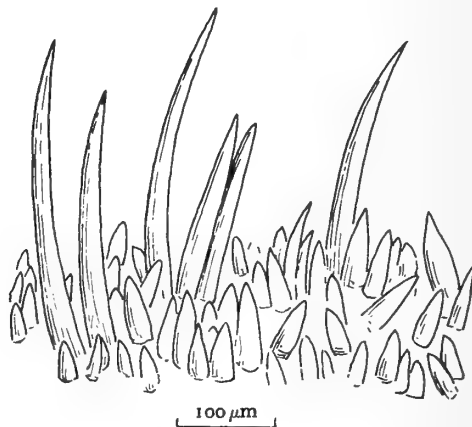


Figure 35

Leptochiton nexus Carpenter, 1864

Girdle scales and spines. Specimen collected at Hyperion stack, Los Angeles, California, at a depth of 62 m (LACM-AHF 5714-38)

On January 6, 1919, BERRY described and figured *Lepidopleurus (Xiphiozona) heathi* [Type locality: Monterey Bay, California]; five months later, on June 7, 1919, DALL published his description of *Lepidopleurus (Leptochiton) ambustus* [Type locality: Santa Barbara Channel, Califor-

nia]. Although WILLETT (1935) regarded these two nominal species as junior synonyms of *Leptochiton nexus*, the taxonomic position of these species has remained uncertain.

The problem was finally solved when, thanks to the unfailing generosity of Dr. Joseph Rosewater, it became possible to examine the holotype of Carpenter's *Lepidopleurus nexus* (USNM 16270) and verify its conspecificity with *Leptochiton heathi* (Berry, 1919) and its already recognized synonym, *Leptochiton ambustus* (Dall, 1919). The specimen (Figures 3 & 4) is accompanied by a label which reads, "Type/Catalina Id., Cooper"; a second label reads: "*Leptochiton nexus* Cpr./Type/Cooper." The specimen, dried and partly disarticulated (loose valve vii, fragment of valve viii, and of valve [?] i), has an estimated length of 7.5 mm. Color brownish gray, except for a longitudinal creamy-white stripe along the jugum. Tegmentum paved with granules, mostly rounded, about 40 μ m in diameter, which tend to align themselves into longitudinal rows in the central areas (about 50 rows per half side), and in radial rows in the lateral areas (about 15 rows per lateral area). Lateral areas not otherwise defined. Jugum subcarinated, most particularly at the apex of the valves. Mucro central. Girdle shows a few short crystalline spicules, interspersed. Color slides of the holotype specimen at CASIZ, Color Slides Series.

The examination of the syntype series of *Lepidopleurus ambustus* Dall, 1919 (USNM 274120), was possible again through the kindness of Dr. Joseph Rosewater. The accompanying label reads, "20-40 f. Sta. Barb. Chan./Sta. Barbara Ids. F. A. Woodworth/Types." The series consists of 3 dried specimens; the largest, here designated as lectotype (Figure 6), measures 17.5 mm in length, 9.0 mm in width, 3.3 mm in height. All specimens show the same slight subcarination, and the same tegmental sculpture seen in the holotype of *L. nexus* (Figure 5). The tegmental granules are generally round, and measure about 40 μ m in diameter. Color slides of the lectotype and paralectotypes, at CASIZ Color Slide Series, Nos. 1928-1930.

The understanding of the species, *Leptochiton nexus*, comes clear from the joint descriptions of CARPENTER in PILSBRY (1892), BERRY (1919), and DALL (1919). However, a few observations must be added: In size, specimens of *L. nexus* do not usually exceed 20 mm; however, an unusually large specimen collected at 12-18 m, off Santa Cruz Island, California (LACM-AHF 1197-40) has an estimated length of 25 mm. Mean width/length ratio, based on 10 specimens from several localities is 0.59.

The color of *Leptochiton nexus* is remarkably constant, a dark tone of brown, often with a lighter creamy-tan stripe along the jugum, and minute specks of a darker brown or

lavender, interspersed. Girdle, distinctly spiculate, with many hyaline spines (up to 400-500 μ m in length) strewn throughout (Figure 35).

The radula is figured here for the first time. In a specimen 7.8 mm long (LACM-AHF 5714-58: "34 fathoms [62 m] 6.25 miles from Hyperion stack, Los Angeles, California, April 18, 1958") measures 5.2 mm in length (66% of the specimen's total length) and has 35 rows of mature teeth. The median tooth (Figure 36) is larger in the front

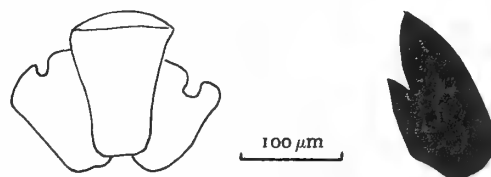


Figure 36

Leptochiton nexus Carpenter, 1864

Radula: Median tooth, first lateral teeth and head of second lateral tooth. Specimen collected at Hyperion stack, Los Angeles, California at a depth of 62 m (LACM-AHF 5714-38)

where it bears a small blade 110 μ m wide. First lateral teeth have a conspicuous notch in the middle of the anterior border. Major lateral teeth have a bicuspid head, which measures about 180 μ m in length, and 90 μ m in width. Outer marginal teeth are about 125 μ m long, 55 μ m wide, with a length/width ratio of 2.27.

Distribution: *Leptochiton nexus* seems to have a continuous distribution from Alaska to Baja California. The verified northernmost record is Cohen Island, Kachemak Bay, Kenai Peninsula, Alaska [59°32.5'N; 151°28.5'W] (LACM 73-20, leg. J. H. McLean & R. Baxter, July 31, 1973, 20+ specimens); the southernmost record, Punta Abreojos, Baja California, Mexico [26°16'N; 113°41'W] (LACM-AHF 1710-49, coll. March 7, 1949). Judging from the available collections, *L. nexus* seems to be easier to find between the latitudes of 45° to 28°N. It has been collected at most offshore islands: Catalina (USNM 16270; USNM 274119; LACM-AHF 2132-52; LACM 32-1), Anacapa (LACM-AHF 874-38), Santa Cruz (LACM-AHF 1155; LACM-AHF 1191-40 D1; LACM 1191-40 D2; LACM-AHF 1197-40; LACM-AHF 1303-41; LACM-AHF 1418-41 D2), Santa Rosa (LACM-AHF 1022; LACM-AHF 995-39) Cedros (LACM-AHF 1253-41; LACM-AHF

1247-41; LACM 71-159), and Natividad (LACM-AHF 1706-49). Recently, *L. nexus* was reported at Bahía de Los Angeles (29°00'N; 133°35'W) in the Gulf of California (HANSELMANN, 1977); thanks to the generosity of Col. G. A. Hanselman, I was given the privilege of examining and verifying the identification of the specimens, one collected by D. Mulliner at 17 m, in May, 1970, another (11.5 mm long) dredged at 90 m by R. Poorman.

Bathymetrically, *Leptochiton nexus* ranges from the intertidal zone to 139-141 m (LACM-AHF 1247-41, off Cedros Island, Baja California, Mexico). Median depth, based on the lots examined, 50 m.

Remarks: *Leptochiton nexus* is much less abundant than *L. rugatus*. It clearly differs from *L. rugatus* by its darker color, larger size, and wider body. A comparison between 10 adult specimens of each species revealed that the mean length/width ratio of *L. nexus* specimens (ratio, 0.59) was significantly greater than that of *L. rugatus* specimens (ratio, 0.53), (Mann-Whitney test, $p < 0.05$ - one-tailed). Differences in the girdle and radular characteristics of the two species were also marked. However, differences in the tegmental sculpture were more difficult to ferret out in view of the considerable intraspecific variation that both species display in the appearance and disposition of the tegmental granules. A relatively reliable observation in the quick differential diagnosis between the two species is the total absence of carination (i.e., a perfectly round back) in *L. rugatus* while subcarination, particularly at the posterior end of the intermediate valves is usually discernible in *L. nexus*.

The synonymy of *Leptochiton lycurgus* Dall, 1919, is based on the examination of the holotype (USNM 274119) available through the courtesy of Dr. Joseph Rosewater. The specimen (Figure 8), dry, curled, is whitish, and slightly carinated; anterior valve is missing; estimated length of the specimen, 7 mm. The accompanying label reads: "Type/

Catalina Id., Dall." In all its characteristics it corresponds to DALL's description (1919: 500). Color slides of the specimen, CASIZ Color Slide Series Nos. 1189-1191.

Leptochiton alveolus (Lovén, 1846)

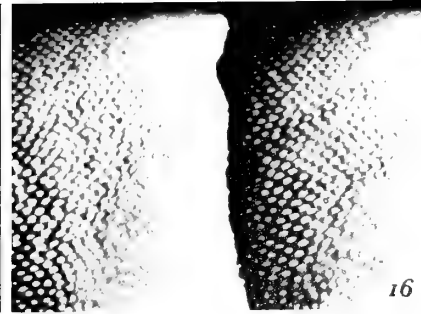
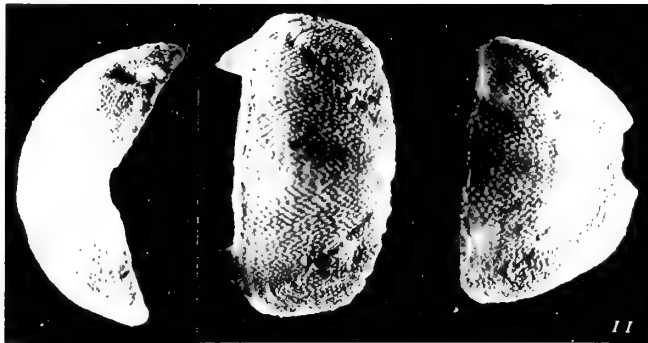
(Figures 9 to 16, 37 and 38)

- Chiton alveolus* LOVÉN, 1846: 159-160 - JEFFREYS, 1882: 668
Lepidopleurus alveolus (Lovén). SARS, 1878: 110; plt. 7, figs. 3a-3i; plt. I, fig. 7 (radula) - PILSBRY, 1892, 14: 6; plt. 2, figs. 23-31 - THIELE, 1902: 282 - NIERSTRASS, 1905: 4-5 - THIELE, 1909: 9; plt. 1, figs. 2-4 - JOHNSON, 1915: 7 - JAKOVLEVA, 1952: 51-52; fig. 18, plt. 1, fig. 6 - LA ROCQUE, 1953: 7 - ABBOTT, 1974: 393
Leptochiton alveolus (Lovén). DALL, 1879b: 317; 1882: 411 - HADDON, 1886: 1, 12-13 - THIELE, 1893: 387; plt. 31, fig. 34
Leptochiton belknapi DALL, 1879a: 1; 1879b: 317-318, 1882: 411 - HADDON, 1886: 1, 10-13; plt. 1, fig. 2, plt. 2, figs. 2a-2d - SMITH, 1947a: 4; 1947b: 17 - BURGHARDT & BURGHARDT, 1969: 23-24 - ABBOTT, 1974: 393
Lepidopleurus belknapi (Dall). PILSBRY, 1892, 14: 7-9; plt. 1, figs. 18-22. NIERSTRASS, 1905: 4-5 - DALL, 1921: 187 (in section *Leptochiton*) - OLDROYD, 1927: 851 (in section *Leptochiton*) - LA ROCQUE, 1953: 8
Leptochiton benthus HADDON, 1886: 1, 10-13; plt. 1, fig. 1; plt. 2, figs. 1a-1m
Lepidopleurus benthus (Haddon). PILSBRY, 1892, 14: 9; plt. 1, figs. 1-13 - NIERSTRASS, 1905: 4-5
Lepidopleurus (*Leptochiton*) *benthus* (Haddon). HANSELMANN, 1977: 62
Lepidopleurus mesogonus DALL, 1902: 555-556; 1921: 187 (in section *Leptochiton*) - OLDROYD, 1927: 852-853 - LA ROCQUE, 1953: 8 - BURGHARDT & BURGHARDT, 1969: 25 - ABBOTT, 1974: 393
Leptochiton mesogonus (Dall). SMITH, 1947a: 4; 1947b: 17
Lepidopleurus halistreptus DALL, 1902: 556; 1908: 218, 354 - THORPE in KEEN, 1971: 882
Lepidopleurus halistreptus abbreviatus DALL, 1908: 354

Explanation of Figures 9 to 16

- Figure 9: *Lepidopleurus farallonis* Dall, 1902. Holotype (USNM 109025)
 Figure 10: *Leptochiton belknapi* Dall, 1879. Holotype (USNM 30972): Close-up to show detail of tegmental sculpture
 Figure 11: *Lepidopleuridus luridus* Dall, 1902. Holotype (USNM 109027: close-up of anterior, intermediate, and posterior valves
 Figure 12: *Lepidopleurus mesogonus* Dall, 1902. Holotype (USNM 109019): Close-up to show detail of tegmental sculpture

- Figure 13: *Lepidopleurus halistreptus* Dall, 1902. Holotype (USNM 109032): Close-up to show detail of sculpture
 Figure 14: *Lepidopleurus simplex* Nierstraß, 1905. Lectotype (herein designated) (ZMA)
 Figure 15: *Lepidopleurus giganteus* Nierstraß, 1905. Lectotype (herein designated) (ZMA)
 Figure 16: Close-up of the specimen in Figure 15 to show detail of tegmental sculpture



- Lepidopleurus abbreviatus* (Dall). THORPE in KEEN, 1971: 882
- Lepidopleurus luridus* DALL, 1902: 556-557; 1908: 218, 355; 1921: 187 (in section *Leptochiton*) – OLDROYD, 1924: 184. 1927: 851-852 (in section *Leptochiton*) – LA ROCQUE, 1953: 8 – BURGHARDT & BURGHARDT, 1969: 24-25 – THORPE in KEEN, 1971: 882 – ABBOTT, 1974: 393
- Leptochiton luridus* (Dall). SMITH, 1947a: 4. 1947b: 17
- Lepidopleurus farallonis* DALL, 1902: 557. 1908: 218-355 – PACKARD, 1918: 291-292 – DALL, 1921: 187 (in section *Leptochiton*) – OLDROYD, 1927: 852 (in section *Leptochiton*) – BURGHARDT & BURGHARDT, 1969: 24 – THORPE in KEEN, 1971: 882 – ABBOTT, 1974: 393
- Leptochiton farallonis* (Dall). SMITH, 1947a: 4. 1947b: 17
- Lepidopleurus giganteus* NIERSTRASS, 1905: 3-4; figs. 1-2, 39-42
- Lepidopleurus simplex* NIERSTRASS, 1905: 4-6; figs. 3, 44-47
- Lepidopleurus opacus* DALL, 1908: 218, 354-355 – THORPE in KEEN, 1971: 882
- Leptochiton opacus* (Dall). SMITH & FERREIRA, 1977: 84; figs. 3, 4
- Lepidopleurus japonicus* THIELE, 1909: 11; plt. 1, figs. 21-29 – TAKI & TAKI, 1929: 162-163 – JAKOVLEVA, 1952: 50-51; fig. 17, plt. 1, fig. 5 – TAKI, 1962: 31 – TAKI, 1964: 408.
- Lepidopleurus japonicus aequivalvus* BERGENHAYN, 1933: 4-5, figs. 1a-1c – TAKI, 1962: 32 – TAKI, 1964: 408
- Lepidopleurus aequispinnus* BERGENHAYN, 1933: 6-8 text figs. 1d-1g; plt. 1, fig. 1; plt. 2, fig. 20 – TAKI, 1962: 32 – TAKI, 1964: 40

Type Material:

Chiton alveolus Lovén, 1846: Unknown, presumably lost or never designated.

Leptochiton belknapii Dall, 1879: Holotype (USNM 30972); locality, "Lat. 58°8' N; Long. 171°19' W."

Leptochiton benthus Haddon, 1886: Holotype (BMNH 1889.11.9.1); locality, HMS *Challenger* station 241, "Lat. 35°41' N; long. 157°42' E." Not examined.

Lepidopleurus mesogonus Dall, 1902: Holotype (USNM 109019); locality, USS *Albatross* station 3342, "off the Queen Charlotte Islands, British Columbia," Canada.

Lepidopleurus halistreptus Dall, 1902: Holotype (USNM 109032); locality, USS *Albatross* station 3415, "off Acapulco, Mexico."

Lepidopleurus luridus Dall, 1902: Holotype (USNM 109027); locality, USS *Albatross* station 3393, at "Panama Bay."

Lepidopleurus farallonis Dall, 1902: Holotype (USNM 109025); locality, USS *Albatross* station 3104, "off the Farallones Islands, near San Francisco, California."

Lepidopleurus giganteus Nierstraß, 1905: Lectotype [herein designated] at Zoologisches Museum of Amsterdam (ZMA); locality, *Siboga* station, 221, "6°24' S, 124°39' W."

Lepidopleurus simplex Nierstraß, 1905: Lectotype [herein designated] at ZMA; locality, *Siboga* station, 88, "0°34.6' N, 119°8.5' W."

Lepidopleurus opacus Dall, 1908: Holotype and paratype (USNM 110664); locality, USS *Albatross* station 4647, "be-

tween the Galápagos Islands and the Peruvian coast."

Lepidopleurus japonicus Thiele, 1909: Types in Zoologisches Museum, Humboldt Universität, Berlin ["1 type specimen from Kaiyama (in alcohol) and 1 set of plates from Enoshima (also marked as a type)," Dr. R. Kilias, *in litt.*, 6 September 1978]. Not examined.

Lepidopleurus japonicus aequivalvus Bergenhayn, 1933: Type at the Zoologiska Museet, Uppsala, Type collection No. 136; locality, Sagami Bay, Japan. Not examined.

Lepidopleurus aequispinnus Bergenhayn, 1933: Type at the Zoologiska Museet, Uppsala, Type collection No. 142; locality, Sagami Bay, Japan. Not examined.

Type Locality: "Boh[us]-Bergen" (LOVÉN, 1846: 159), Scandinavia.

Original Description: "210. *C. alveolus* Sars ms. — *T. oblonga*, convexa, alba, squamulis limbi inaequalibus, angustis; 12/5 mm — *T. satis convexa*, vix culminata; valv. 8, 1, 7, 2, 3, 6, 4, 5, arcuatae, longae, long. ad lat. in quinta = 1:3, postico rectae, vix mucronatae, margine antico leviter arcuato, medio emarginato, limbali rotundato. V. secundo antico subangulata, prima semicircularis, ultima subelliptica. Laminae spatio separatae 1/3 tot. lat. fere superante, rotundatae. Series granulorum in areis lateralibus transversae, densae, fere secundum strias incrementi arcuatae. Limbus albus, angustus, tenuis, squamis elongatis, mucronatis irregulariter imbricatus. Boh.-Bergen." (LOVÉN, 1846: 158-159).

Extended Description: SARS (1878) figured the species (*op. cit.*: plt. 7, figs. 3, a-i), and added to the description: "*Corpus colore nunc pallidiore, albido-cinereo, nunc obscuriore, interdum fere omnino nigro, forma quam solito angustiore, elongato-oblongum, plus duplo longius quam latius, zona perangusta, squamulis inaequalibus, nonnullis spinaeformibus. Testa sat convexa, dorso aequaliter arcuato ne vestigium quidem carinae vel arearum lateralium praebente, valvulis sat elongatis, postica antica majore, semiorbiculari, antice ad lineam rectum truncata, mediis subaequalibus, margine postico recto, antico medio leviter emarginato. Superficies valvularum tuberculis minutis ovatis regulariter dispositis ubique sculpta. Long. 16 mm*" (*op. cit.*: 110-111).

PILSBRY (1892, 14: 6) translated part of Sars' description and reprinted his illustrations of the species (*op. cit.*: plt. 2, figs. 23-31). The radula, first figured by SARS (1878: plt. I, fig. 7) was again described and illustrated by THIELE (1893: 387; plt. 31, fig. 34), and JAKOVLEVA (1956: 51-52; text fig. 18). THIELE (1909: 9; plt. 1, figs. 2-4) enlarged upon the description of the girdle scales.

From this study of several lots of *Leptochiton alveolus* (LOVÉN, 1846) in the eastern Pacific, the following observations must be added: Shell uniformly colored, creamy

white to a light tan; occasional specimens may show orange or black, bituminous-looking deposits. Length, often over 3 cm; the largest specimen examined (CASIZ 008945, Oregon coast, 1829 m), if fully extended, it is estimated to measure over 40 mm in length. One of the specimens described by NIERSTRASS (1905) as *L. giganteus* is reported to be 43 mm long. Based on 10 specimens from several localities, the mean width/length ratio is 0.39. Valves high arched, subcarinated to markedly carinated; jugal angle, also quite variable, often less than 90° . In young (small) specimens the valves may be slightly beaked. Mucro central to slightly posterior, often elevated.

Tegmental surface covered throughout with granules, round to oval, and disposed in quincunx; the granules are usually well defined and clearly separated by a space about equal to their diameter. In size, shape, and degree of separation from each other, the granules vary considerably among specimens. As a rule, the tegmental granules tend to be smaller and more crowded together in the lateral than in the central areas. Lateral areas otherwise poorly defined in most specimens; however, they may be slightly elevated, or vaguely demarcated by a shallow sulcus. Concentric growth lines, in the form of 3 or 4 rugae, are often seen in the lateral areas, quite conspicuously so in some specimens. Anterior valve, and postmucro area of posterior valve may also show similar growth lines, as well as crowded and smaller sized tegmental granules.

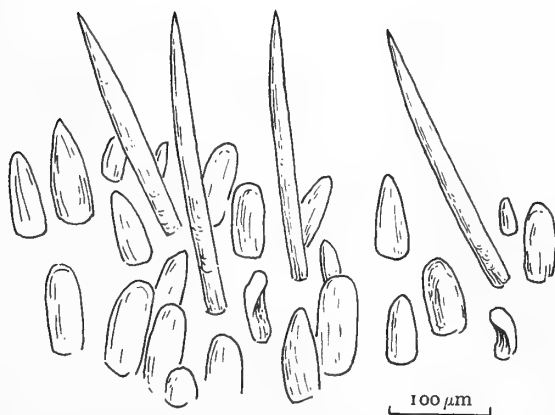


Figure 37

Leptochiton alveolus (Lovén, 1846)

Girdle scales and spines. Specimen collected off Catalina Island, California, at a depth of 550 m (LACM-AHF 1427-41)

Girdle relatively narrow, covered by somewhat polymorphic scales, mostly conical (up to $100\ \mu\text{m}$ in height, $30\ \mu\text{m}$ in diameter), displaying a few variably marked longitudinal striations (Figure 37); interspersed, there are a variable number of long, pointed, hyaline spines, up to $300\ \mu\text{m}$ in length. In this respect, *Leptochiton alveolus* specimens seem to be quite variable, even within the same collection site inasmuch as some may have a conspicuously large number of spines (ca. $100/\text{mm}^2$), while others may show only very few (ca. $10/\text{mm}^2$) or, perhaps, even none.

The radula of a specimen 23 mm long (LACM-AHF 1427-41, off Catalina Island, California, at 550 m) measures $10.0\ \text{mm}$ in length (43% of the total specimen's length), and has 45 rows of mature teeth. Median tooth, rectangular, slightly large in the front where it bears a thin blade, $180\ \mu\text{m}$ wide (Figure 38). First lateral teeth rectangular, with

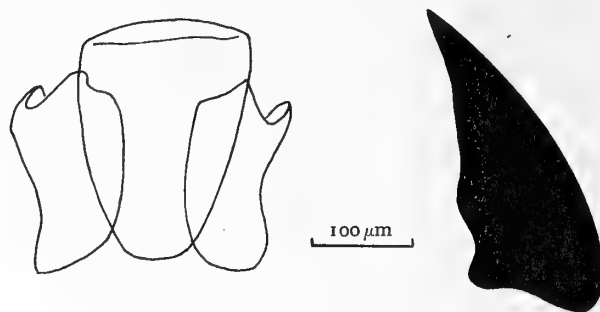


Figure 38

Leptochiton alveolus (Lovén, 1846)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected off Catalina Island, California, at a depth of 550 m (LACM-AHF 1427-41)

slightly arcuate outer edge. Second (major) lateral teeth with unicuspid head which measures about $300\ \mu\text{m}$ in length, $140\ \mu\text{m}$ in width; the head's outer edge is smoothly convex, but its inner edge displays a small bump (not quite a denticle) at its middle point, as illustrated in Sars (1878), Thiele (1893), and Jakovleva (1952). Outer marginal teeth measure about $220\ \mu\text{m}$ in length, $150\ \mu\text{m}$ in width, with a length/width ratio of 1.46.

Distribution: *Leptochiton alveolus* (Lovén, 1846) has long been considered a North Atlantic species ranging from Scandinavia and the Bay of Biscay in the east, to the Gulf of St. Lawrence and the Gulf of Maine in the west. Jakovleva (1952) acknowledged its presence in the Sea of Okhotsk, along the eastern coast of U.S.S.R. This study

establishes the presence of *L. alveolus* in the eastern Pacific, as well as in the Sea of Japan and the Bering Sea.

From the data listed in Table 1, the northernmost record of *Leptochiton alveolus* in the eastern Pacific is 58°08'N

(USNM 30972: *L. belknapi* Dall, 1919, holotype); the southernmost record, 4°33'N (USNM 110664: *L. opacus* Dall, 1919, holotype and paratype). It has been collected in the Philippine Islands, at 1911 m, by the HMS *Challenger*

Table 1

Lots of *Leptochiton alveolus* (Lovén, 1846) examined, with latitudes, number of specimens per lot, maximum length of specimens in the lot, and collecting depth.

Lot	Latitude	Number of spms. per lot	Max. length of spm. in lot mm	Depth m
USNM 30972, <i>L. belknapi</i> , Type	58°08' N	1	15	1 840
USNM 109019, <i>L. mesogonus</i> , Type	53°00' N	1	30	2 906
LACM 67-35	49°43' N	1	10	164
Cowan Coll. No. 5374 (Univ. Brit. Columbia)	48°02' N	2	10	977
CASIZ [R/V <i>Ancona</i>]	44°38'-40' N	20	15	800-2 000
CASIZ 008945, R/V <i>Ancona</i>	44°31' N	5	40	1 829
CASIZ [USS <i>Mulberry</i> ; R/V <i>Scofield</i>]	37°48' N	7	20	732-2 104
USNM 109025, <i>L. farallonis</i> , Type	37°45' N	1	10	715
CASIZ 002893	36°47' N	8	20	567-640
CASIZ 009515	36°45' N	6	21	954-1 044
CASIZ 009524	36°45' N	1	15	166
LACM 60-21	36°38' N	1	11	183
LACM 63-52	36°38' N	1	12	183
LACM-AHF 1471-41	33°34' N	1	23	523-549
LACM-AHF 1400-41-D1	33°24' N	1	24	417
LACM-AHF 1156-40	33°24' N	2	15	421-695
LACM-AHF 1306-41-D1	33°24' N	1	20	417-488
LACM-AHF 2004-50	33°24' N	1	13	439-457
LACM-AHF 1425-41	33°13' N	1	15	512
LACM-AHF 1019-39	33°04' N	1	20	457-549
CASIZ 009521 (Gulf of California)	22°48' N	1	10	366-1 336
CASIZ 009520	21°25' N	4	15	3 000
USNM 109032, <i>L. halistreptus</i> , Type	16°51' N	1	30	3 437
SDNH 68405	15°00' N	1	8	3 962
USNM 109027, <i>L. luridus</i> , Type	8°50' N	1	15	1 866
USNM 110664, <i>L. opacus</i> , Type	4°33' N	2	35	3 667
ZMA, <i>L. simplex</i> , Type	0°35' N	1	7	1 301
ZMA, <i>L. giganteus</i> , Type	6°24' S	1	24	2 798
CASIZ 009516 [ex Golikov, USSR]	Kurile Is.	1	10	?
CASIZ 009517 [ex Golikov, USSR]	Bering Sea	1	12	?
CASG 52423 [USS <i>Albatross</i>]	Hokkaido,	2	20	320
	Japan			
CASIZ 001818 [ex Sirenko, R/V <i>Vityaz</i>]	Honshu,	1	20	2 500
	Japan			
B. Sirenko Colln.	Barents Sea	1	12	155
P. Kaas Colln.	Norway	1	10	100
R. Van Belle Colln.	Gulf of	1	8	1 886
	Biscay			

(Haddon, 1886, as *L. belknapi*). The presence of *L. alveolus* in the southern hemisphere cannot be considered sufficiently documented at this time, except for NIERSTRASS' (1905) report of 3 specimens of what he named *Lepidopleurus giganteus*, collected by the *Siboga* (Station 221: 6°24' S, 124°39' W, at 2798 m).

The bathymetric range of *Leptochiton alveolus* in the eastern Pacific based upon the specimens examined in this study, extends from 164 m to 3962 m, with a median of 550 m, which places the species favored habitat in the upper bathyal to lower bathyal or abyssal zone (HEDGPETH, 1957).

Remarks: Until now, *Leptochiton alveolus* was known with certainty only in the North Atlantic. Its presence in the Pacific is firmly established here with the examination of Dall's several eastern Pacific types of *Leptochiton* species made available for study through the generosity of Dr. Joseph Rosewater. An account of Dall's type specimens, and their photographs are given here for the first time.

Leptochiton belknapi Dall, 1874: Holotype (USNM 30972). Accompanying labels read: "1006 fms. sd. & sh./ Lat. 58°8' N., Long. 171°19' W, Belknap," and "Type." A single specimen (Figure 10) dried, curled, carinated, valves slightly beaked, whitish color. Estimated length 15 mm, width 6 mm, height 3.5. Tegmental granules in quincunx throughout. Lateral areas not raised, defined by faint diagonal sulcus, with coarse concentric growth lines. Mucro central. Girdle covered with small spicules crowded together. Two discrepancies in previous descriptions must be noticed: DALL (1874) gives the size of the specimen as "Lon. 10, lat. 3 mm," much smaller than my estimate; and PILSBRY (1892) gives locality longitude as 17°, an obvious typographical error for 171° as stated by Dall, and written on the specimen's label. Color slides at CASIZ Color Slides Series.

Lepidopleurus mesogonus Dall, 1902: Holotype (USNM 109019). Labels read: "Sta. 3342, 1588 fms. ooze, 53°.3/ British Columbia off Q. Charl. Ids." and "Type." A single specimen (Figure 12), dried, dirty white, curled, strongly carinated. Estimated length 30 mm, width 10 mm, height 7 mm; jugal angle about 80°. Strong concentric growth lines in lateral areas and continuing into adjacent pleural area. Mucro central. Girdle sandy looking, with many small spicules interspersed. Color slides at CASIZ Color Slides Series.

Lepidopleurus halistreptus Dall, 1902: Holotype (USNM 109032). Labels read: "Sta. 3415, 1879 fms., m. 36° off Acapulco," and "Type." A single specimen (Figure 13), dried, curled, whitish in color, strongly carinated. Jugal angle about 90°. Estimated length 30 mm, width 10 mm, height 7 mm. Valves i, vii, and viii disarticulated. Lateral areas faintly defined by a diagonal sulcus. Mucro slightly posterior. Girdle arenaceous looking, with spicules (up to 500 µm long) interspersed. Color slides at CASIZ Color Slides Series.

Lepidopleurus luridus Dall, 1902: Holotype (USNM 109027). Labels read: "Sta. 3393, 1020 fms., m. 36°.8," "Panama Bay," and "Type." Single specimen (Figure 11), dried, curled, whitish, carinated (but less so than in the previously mentioned type specimens). Estimated length 15 mm, width 6 mm, height 3 mm. Valves i, vii, and viii disarticulated. Tegmental granules relatively larger and more widely separated than in above mentioned type specimens. Lateral areas modestly defined and raised, with a few concentric growth ridges. Posterior valve distinctly longer than anterior valve, with a truncated looking anterior edge. Girdle sandy looking, with occasional spicules interspersed. Color slides at CASIZ Color Slides Series.

Lepidopleurus farallonis Dall, 1902: Holotype (USNM 109025). Labels read: "Sta. 3104, 391 fms. coral, 41° off the Farallones," and "Type." Single specimen (Figure 9),

Explanation of Figures 17 to 24

Figure 17: *Hanleyella oldroydi* (Dall, 1919). 6.2 mm long. Monterey Bay, California (LACM 63-50)

Figure 18: Close-up of specimen in Figure 17 to show detail of central area, lateral areas, and girdle

Figure 19: *Lepidopleurus oldroydi* Dall, 1919. Holotype (USNM 218767)

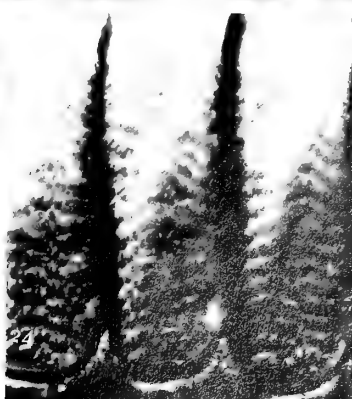
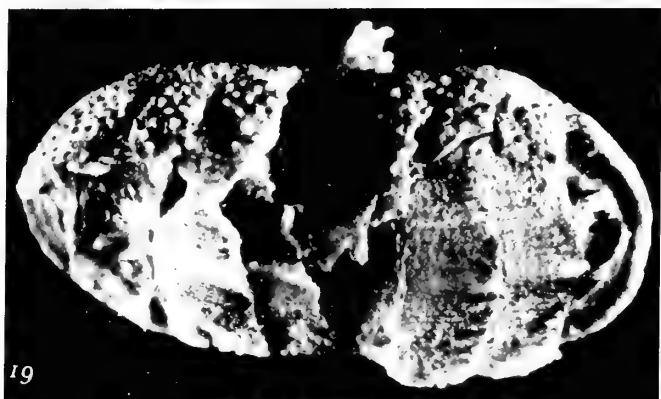
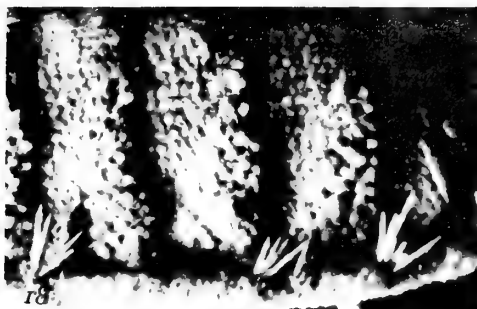
Figure 20: *Oldroydia percrassa* (Dall, 1894). 26 mm long (dried). Catalina Island, California (AJF collection)

Figure 21: *Leptochiton diomedae* Berry, 1917. Holotype (USNM 215625): Close-up of anterior, posterior, and intermediate valves

Figure 22: Close-up of specimen in Figure 21 to show detail of the tegmental sculpture of intermediate valves

Figure 23: *Lepidopleurus lineatus* Nierstraß, 1905. Lectotype (herein designated) (ZMA)

Figure 24: Close-up of specimen in Figure 23 to show detail of tegmental sculpture



dried, curled, whitish, carinated. Valve i fragmented; valve ii broken but in place; valve viii disarticulated. Tegmental granules about 60-80 μm in diameter; average space between granules in the central areas, 20-30 μm . Girdle with numerous spicules (measuring up to 200 μm in length) interspersed. Color slides at CASIZ Color Slides Series.

Lepidopleurus giganteus Nierstrass, 1905: The specimen examined on a loan arranged through the kindness of Dr. H. E. Coomans, Curator of Malacology, Zoologisch Museum of Amsterdam (ZMA) is well preserved in ethyl alcohol. The specimen, marked "Type," conforms well with the description given by NIERSTRASS (1905). It is accompanied by a museum label which reads "*Lepidopleurus giganteus* Nierstr./Stat. 221/figured specimen by Schepman/ fig. 1 & 2," a reference to the illustrations in "Die Chitonen der Siboga-Expedition" (1905). The specimen, the smallest of the 3 specimens found at the Station 221 of the *Siboga* expedition, measures 24.2 mm in length, and 8.2 mm in width, including girdle. It is here designated as lectotype, and illustrated (Figures 15 & 16). The other two specimens of the syntype series of *L. giganteus* are also in the repository of the Zoologisch Museum of Amsterdam (Dr. H. E. Coomans, *in litt.*, June 13, 1978). Color slides of the lectotype at CASIZ, Color Slides Series.

Lepidopleurus simplex Nierstraß, 1905: A specimen marked "Type" examined also through the generosity of Dr. H. E. Coomans (ZMA). The accompanying label reads "*Lepidopleurus simplex* Nierstr./Stat. 88/1 specimen." The specimen, preserved in ethyl alcohol, measures 7.2 mm in length, 3.3 mm in width; it conforms well to NIERSTRASS' (1905) original description. Of the 20 specimens of *L. simplex* mentioned in the *Siboga* Report (1905), 18 are in the Zoologisches Museum of Amsterdam, "one in the Mus. of Brussels, [and] one probably was kept by Nierstraß. We are not able to recognize the figured [in the *Siboga* Report] specimen" (Dr. H. E. Coomans, *in litt.*, June 13, 1978). The examined specimen is here illustrated (Figure 14), and designated as lectotype. Color slides at CASIZ Color Slides Series.

Lepidopleurus opacus Dall, 1908: Holotype and paratype (USNM 110664) examined through the generosity of Dr. Joseph Rosewater. Labels read, "Sta. 4647, 2005 fms., ooze, 35.4°/near Galápagos Ids./off Peruvian coast/Lat. 4°33'S/Lon. 87°42'W," and "Types." Specimens dried, curled, sharply carinated. Photograph of holotype in SMITH & FERREIRA (1977, figs. 3 & 4). Color slides, CASIZ Nos. 1581 (holotype), and 1582-1583 (paratype).

The placement of *Leptochiton benthus* Haddon, 1886, *Lepidopleurus japonicus* Thiele, 1909, and *Lepidopleurus aequispinnus* Bergenhayn, 1933, in the synonymy of *Leptochiton alveolus* (Lovén, 1846) is based on the published

descriptions and illustrations of the respective nominal species; examination of the respective types was not undertaken.

Leptochiton albemarlensis Smith & Ferreira, 1977

Leptochiton albemarlensis SMITH & FERREIRA, 1977: 83-84; figs. 1, 2.

Type Material:

Holotype (CASG, Type Collection No. 58247), and paratype (CASG, Type Collection No. 58248).

Type Locality: Tagus Cove, Isla Isabela (Albemarle Island), Galápagos Archipelago, Ecuador [0°16'S; 91°22'W], dredged at 20 m.

Remarks: The species is known only from the type locality and the type material. On account of its spiculate girdle, *Leptochiton albemarlensis* is similar to *L. nexus* from which it differs by (1) its white color, (2) the quincunx arrangement of the tegmental granules with only a vague tendency to align themselves in diagonal (not longitudinal) rows, and (3) the round back, i.e. with no trace of carination. Compared to *Leptochiton alveolus*, the Galapagan *L. albemarlensis* differs by (1) its round back, (2) the tendency of the tegmental granules to align in diagonal rows, and (3) its much wider body, as revealed by a width/length ratio (for the holotype) of 0.55. CASIZ Color Slides Nos. 1978-1979.

Leptochiton incongruus (Dall, 1908)

(Figure 29)

Lepidopleurus incongruus DALL, 1908: 218, 355 - THORPE in KEEN, 1971: 882.

Type Material:

Holotype (USNM 122969)

Type Locality: "U.S.S. *Albatross*, station 3354 [7°09'45" N; 80°50'00"W], Feb. 23, 1891, Gulf of Panama, in 322 fathoms [589 m]" (DALL, 1908: 355).

Original Description: "Animal with the gills forming a very short posterior row; girdle narrow with extremely minute, close-set spines, giving the effect of a naked, velvety surface. Intermediate valves pale brown, the median line slightly obtusely angular; jugum slightly mucronate behind, the jugal area sculptured with very fine, close-set, rounded, longitudinal threads; pleural tracts with ten or twelve larger threads with wider, flat interspaces, the threads sometimes breaking off abruptly, leaving double-width interval the rest of the way; lateral areas prominent,

very finely granulose, conspicuously concentrically rippled; anterior plate with feeble concentric ripples and similar granulation; posterior valve with prominent subcentral mucro, the central area sculpture like the anterior valve; penultimate valve with a length of 2.3, a width of 6.0, and an altitude of 2.5 mm. Articulations as usual in the genus." (DALL, 1908: 355).

Extended Description: Thanks to the generosity of Dr. Joseph Rosewater of the National Museum of Natural History, the holotype of *Lepidopleurus incongruus* Dall, 1908 was studied and photographed. It is figured here for the first time (Figure 29). The specimen, a bit curled, preserved dry, has a uniform light beige color. Estimated length, 12 mm; it measures 5.5 mm in width, 3 mm in height. Valves moderately carinated, slightly beaked. Lateral areas distinctly defined, moderately raised. Central areas with small, flat-topped granules, arranged in longitudinal rows which converge anteriorly; in the pleural areas, these rows become well defined ridges, about 8-10 per side. Lateral areas, valve i, and postmucro area of valve viii display strong concentric growth wrinkles. Mucro central, not prominent; postmucro moderately concave. Girdle has a sandy appearance, with many short spicules, and a few longer spicules interspersed. Color slides of the holotype at CASIZ Color Slides Series.

Distribution: In addition to the type locality, Panama Bay, *Leptochiton incongruus* was also found off Salina Cruz, Gulf of Tehuantepec, Mexico [15°40'N; 95°20'W] at 3541-3612 m of depth (CASIZ 009525, Scripps coll., 18 Nov. 1958, Loc. No. P-127-58, To 58-2, D-4), 2 specimens, preserved in alcohol, a bit curled, both measuring an estimated 15 mm in length, and beige in color. (CASIZ Color Slides Nos. 724-726).

Remarks: There can be no question that *Leptochiton incongruus* is a valid species, characterized, as Dall (1908) noted, by "a unique sculpture."

Hanleyella Sirenko, 1973

Definition: Central areas with rows of flat granules separated from each other by spaces larger than their diameters. Girdle with spicules, and by a large number of long spines. Inner edge of sutural laminae slope gently relative to the front border of valve. No insertion plates. Radula with tricuspid major lateral teeth.

Type Species: *Hanleyella asiatica* Sirenko, 1973, by OD.

Remarks: *Hanleyella asiatica*, described from Simusir in the Kurile Islands, and *H. oldroydi* (Dall, 1919), from the northeastern Pacific, are the only two known representatives of the genus which SIRENKO (1973) suggests to be "a link between the genera *Lepidopleurus* Risso and *Hanleya* Gray."

Hanleyella oldroydi (Dall, 1919)

(Figures 17 to 19, 39 and 40)

Lepidopleurus (*Leptochiton*) *oldroydi* DALL, 1919: 500-501
Lepidopleurus oldroydi DALL, 1921: 187 (in section *Leptochiton*) - OLDROYD, 1927: 850 (in section *Leptochiton*) - ABBOTT, 1974: 393
Leptochiton oldroydi (DALL). SMITH, 1947a: 6. 1947b: 17 - SMITH & GORDON, 1948: 205 - BURGHARDT & BURGHARDT, 1969: 26
Hanleyella oldroydi (DALL). SIRENKO, 1973b: 1569

Type Material:

Holotype (USNM 218767)

Type Locality: "Monterey, California [36°45'N; 121°55'W]" (DALL, 1919: 501).

Original Description: "Chiton white, with a blackish spot on either side of the jugal area, strongly sculptured; back moderately arcuate, anterior valve semicircular, sculptured with irregularly disposed small prominent round pustules; posterior valve with subcentral prominent mucro, the central area granulose, the periphery pustulose; intermediate valves with axially punctostriate jugal area, lateral areas prominent by reason of the conspicuous pustules which are relatively large for the size of the animal; the pleural tracts coarsely axially grooved, the grooves more or less distinctly punctate; girdle with crowded minute spines of equal length, giving an arenaceous effect; interior whitish, the jugal sinus wide with a straight edge, the sutural laminae small, subtriangular. Length of dry animal, 5; width, 2; height, 0.7 mm." (DALL, 1919: 500-501).

Extended Description: The examination of the holotype (USNM 218767), available through the kindness of Dr. Joseph Rosewater, disclosed the following points not included in, or differing from Dall's original description: The labels accompanying the specimen read "Monterey Harbour/West Coast, California," and "Type." The single specimen (Figure 19) dried, partly disarticulated, has an estimated length of 5.3 mm. The five anterior valves are broken but in place, except for large fragments of valves i

and iv which are available but detached from the specimen; valve vii, disarticulated. Valves moderately carinated, slightly beaked. Pleural areas display about 12 ridges per side. Girdle shows a couple of long spines, about 0.2 mm in length, on the right side of the specimen. Valves show no slits or insertion plates. Color slide of the holotype at CASIZ Color Slides Series No. 1926.

Specimens of *Hanleyella oldroydi* are very small; the largest examined measures 8.2 mm in length, 4.3 mm in width, 1.9 mm in height (LACM 63-26). Specimens are usually high arched, moderately carinated (Figures 17 & 18). Valve i, postmucro area of valve viii, and lateral areas of intermediate valves display large round tubercles, randomly distributed. Central areas of intermediate valves have granules that align themselves in up to 15 rows or ridges which run parallel to the jugum, or diverge forward slightly. Mucro relatively high, slightly anterior. Girdle (Figure 39) covered with minute scales, about $60 \times 30 \mu\text{m}$ in size, which show some irregular striae; in addition there are numerous spinules interspersed, and rather large hyaline spines. These large spines (often $400 \mu\text{m}$ in length by

that, in my experience, these long spines break rather easily in dry specimens, and seem to disappear in OHK solutions.

The radula of a specimen 8.2 mm long (LACM 63-26, Hope Island, British Columbia, leg. I. McT. Cowan & J. H. McLean, on *Ekholi*, May 22, 1963, at 39-90 m) measures 3.5 mm in length (42% of the total specimen), and has 45 rows of mature teeth. Median tooth (Figure 40), rectangular,

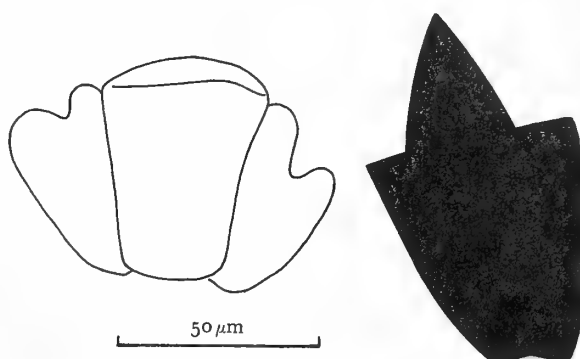


Figure 40

Hanleyella oldroydi (Dall, 1919)

Radula: Median tooth, first lateral teeth, and head of second lateral tooth. Specimen collected at Hope Island, British Columbia, at a depth of 39-90 m (LACM 63-26)

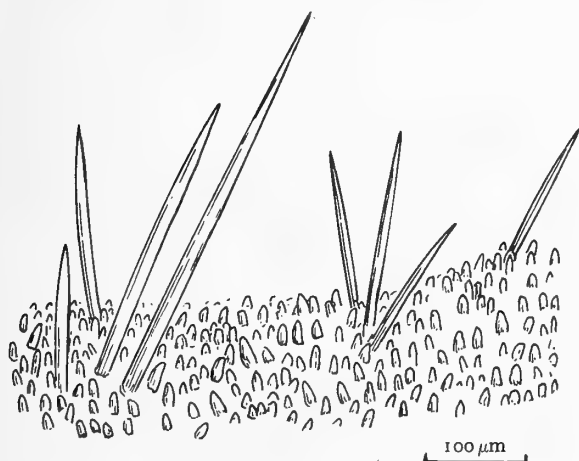


Figure 39

Hanleyella oldroydi (Dall, 1919)

Girdle scales and spines. Specimen collected at Hope Island, British Columbia, at a depth of 39-90 m (LACM 63-26)

$30 \mu\text{m}$ in width) are mostly interspersed throughout the girdle, although with a definite tendency to bunch up and be larger at the sutures, and close to the margin of the girdle where they may constitute (particularly in young specimens) a conspicuous marginal fringe. It is worth noting

slightly wider in front than in back, maximum diameter at anterior blade, $42 \mu\text{m}$. First lateral uncharacteristic except perhaps by the presence of a notch in the middle of anterior edge. Second (major) lateral with a tricuspid head which measures about $100 \mu\text{m}$ in length, and $45 \mu\text{m}$ in width. Outer marginal teeth, $58 \mu\text{m}$ long, $35 \mu\text{m}$ wide; length/width ratio 1.65.

Distribution: BURGHARDT & BURGHARDT (1969), SIRENKO (1973), and ABBOTT (1974) stated that the range of *Hanleyella oldroydi* extends to Alaska. In this study the northernmost verified record is Edna Bay, Kosciusko Island, Alaska [$55^{\circ}57'N$, $133^{\circ}40'W$] (CASG 32430, leg. G. D. Hanna, July, 1947); the southernmost record, Cabo San Quintín, Baja California, Mexico ($30^{\circ}17'40''N$; $115^{\circ}54'40''W$) (LACM 71-150, leg. J. H. McLean & P. LaFollette, *Searcher*, Sta. 226-227, October 17, 1971, at 36-55 m). The species has been collected at Monterey Bay (LACM 60-21, LACM 60-22, LACM 60-24, LACM 63-50, LACM 66-56), Catalina Island (LACM A.375, LACM 32-1, LACM 65-6, LACM-AHF 1323-41, LACM-AHF 1350-41, LACM-AHF 1430-41 D1, LACM-AHF 1523-41), San

Clemente Island (LACM-AHF 911-39), and Santa Rosa Island (LACM-AHF 1290-41).

Hanleyella oldroydi is a relatively deep water species; the recorded bathymetric range is from 18 m (LACM 60-22) to 420-455 m (LACM-AHF 1992-50); the median depth, based on the lots examined, at about 100 m.

Remarks: From the original description and illustrations of *Hanleyella asiatica*, and from the examination of specimens generously donated by Dr. B. Sirenko, Zoological Institute, Academy of Sciences of U.S.S.R., Leningrad, *H. oldroydi* is found to differ clearly from its western Pacific counterpart by 1) a much stronger tegmental sculpture, 2) the granulose aspect of the pleural ridges (almost smooth in *H. asiatica*), 3) the frankly pustulose lateral areas (almost sculptureless in *H. asiatica*), and 4) the tendency of the long girdle spines to bunch up in tufts (a tendency not noticed in the specimens of *H. asiatica* examined). In addition, while females of *H. asiatica* are known to carry young specimens in the mantle cavity (SIRENKO, 1973), the brooding habit has not been observed in *H. oldroydi*.

Oldroydia Dall, 1894

Definition: "Valves heavy, strongly sculptured, with irregular transverse ribs that in life are well separated by narrow extensions of girdle reaching to jugum, resulting in coverage that is partial to apical only; articulamentum well developed, unslit; tegmentum with posterior extension between rather large sutural laminae; jugal area prominent, sculptured differently from pleural areas; lateral areas not differentiated." (SMITH, 1960: 52). First described as a section of *Lepidopleurus*; elevated to generic rank by THIELE (1910).

Type Species: *Lepidopleurus (Oldroydia) percrassus* Dall, 1894, by OD.

Remarks: For its heavy and strongly sculptured valves, the monotypic genus *Oldroydia* Dall bears close affinity to *Lepidopleurus* Risso of which it may be considered to be the Pacific counterpart.

Oldroydia percrassa (Dall, 1894)

(Figure 20)

Lepidopleurus percrassus DALL, 1894: 90-91 (in new section *Oldroydia*)

Lepidopleurus (Oldroydia) percrassus DALL. BERRY, 1907: 47
Oldroydia percrassa (Dall). THIELE, 1910: 71, 105; pl. 7, figs.

1-8 - DALL, 1921: 187 - OLDROYD, 1927: 854-855 - STRONG, 1937: 194 - BURCH, 1942: 7 - BURCH & BURCH, 1943: 5 - SMITH, 1947a: 7. 1947b: 18 - SMITH & GORDON, 1948: 205 - JAKOVLEVA, 1952: 52-53; text. fig. 19; pl. 19, fig. 1 - TAKI, 1964: 408 - BURGHARDT & BURGHARDT, 1969: 33; pl. 4, fig. 68 - ABBOTT, 1974: 393

Hanleya hanleyi (Bean). OLDROYD, 1927: 855 - SMITH, 1947a: 7. 1947b: 18 - SMITH & GORDON, 1948: 205 - JAKOVLEVA, 1952: 54. [not *Chiton hanleyi* BEAN in THORPE, 1844]

Hanleya spicata BERRY, 1919: 8-10; pl. 1, fig. 3; text figs. 5-6 - SMITH, 1947a: 7. 1947b: 18 - SMITH & GORDON, 1948: 205

Hanleya hanleyi spicata BERRY. DALL, 1921: 188 - OLDROYD, 1927: 855-856.

Type Material:

Lepidopleurus percrassus Dall, 1894: Holotype, "larger, partially disarticulated specimen marked 'type'", and 2 paratypes (USNM 107274) (Dr. J. Rosewater, *in litt.*, 3 April, and 27 July 1978). Paratypes (CASG-SU Type no. 6239), 5 specimens.

Hanleya spicata Berry, 1919: Holotype (S. S. Berry private colln., Cat. No. 4102); "off Point Pinos, Monterey Bay, California." Not examined.

Type Locality: "Specimens obtained by Mr. T. S. Oldroyd from a stone pulled up from about 75 fathoms [137 m] in the Santa Barbara Channel off San Pedro [33°45'N; 118°11'W], California" (DALL, 1894: 91).

Explanation of Figures 25 to 32

Figure 25: *Lepidopleurus nicomedes* Dall, 1919. Holotype (USNM 96935): anterior valve

Figure 26: Lateral view of the specimen in Figure 25

Figure 27: Posterior view of the specimen in Figure 25

Figure 28: *Lepidopleurus agesilaus* Dall, 1919. Lectotype (herein designated) (USNM 96227)

Figure 29: *Lepidopleurus incongruus* Dall, 1908. Holotype (USNM 122969)

Figure 30: *Lepidopleurus rissoi* Nierstraß, 1905. Lectotype (herein designated) (ZMA)

Figure 31: Close-up of the specimen in Figure 30 to show detail of lateral and central areas

Figure 32: Posterior valve of specimen in Figure 30



Figure 25



Figure 26



Figure 27

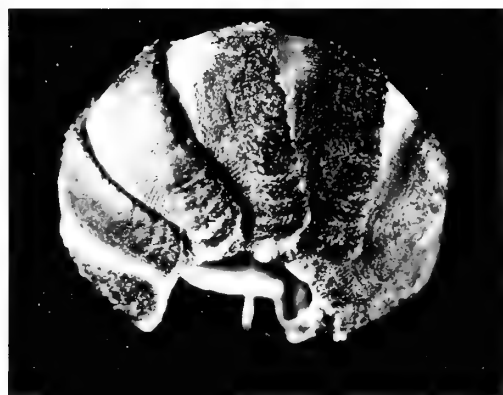


Figure 28

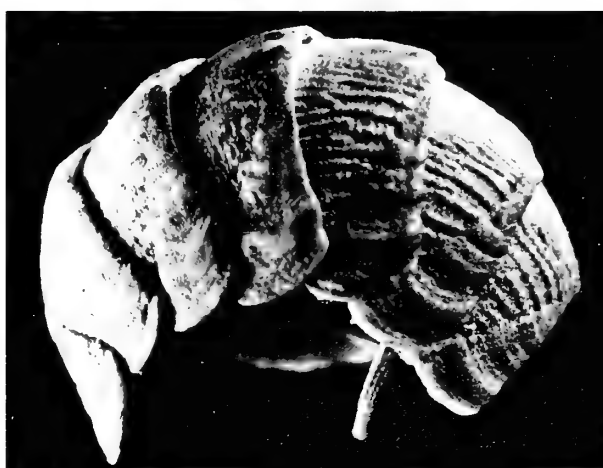


Figure 29



Figure 30



Figure 31

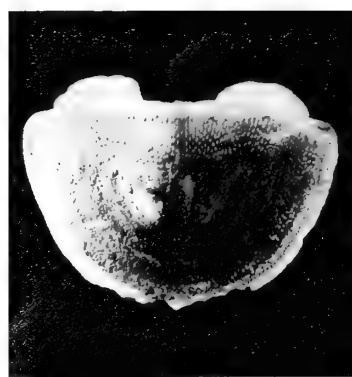


Figure 32

Original Description: "Shell solid, strong, small, of a pale pinkish-brown with a darker brownish girdle which appears rather narrow in the dry state; scales very minute, partly dehiscent, chaffy, with occasional slender spinules resembling hairs; scales on the base crowded, minute, sandy; an extension of the girdle is prolonged between the valves on each side as far as the jugum, the surface of these sinuses is also minutely scaly with occasional spinules; valves thick, white below, moderately arched with the prominent jugum forming a sort of keel; near the points of insertion the valves are heavily callous below; the sutural laminae are short, smooth and separated at the median sinus by a prolongation of the jugum in advance of the anterior margins of the pleurae; sculpture of the jugum consisting of punctate fore-and-aft parallel grooves with some small elevated transverse ridges anteriorly; the rest of the valve has, on each side, six or eight vermicular ridges diverging toward the posterior edge of the valve and irregularly corrugated with sharp, fine, elevated lamellae crossing the interspaces transversely, but fading out on the ridges; head-valve highest at the subcentral, not very prominent mucro, in front sculptured like the head-valve. Length about 14, width 5.75, height 2.5 mm, in the dry state. The dry girdle about half a millimeter wide." (DALL, 1894: 90-91).

Extended Description: *Oldroydia percrassa* was first figured by THIELE (1910) who added some important details to Dall's description. Thiele described the girdle as covered with small spinules, about 100 μ m long by 10 μ m thick (*op. cit.*: fig. 6) with much larger spines, about 400 μ m long by 40 μ m thick, interspersed; the underside of the girdle, covered by simple scales, about 18 μ m wide, ending in a point (*op. cit.*: fig. 7). Thiele also illustrated the radula, with its relatively wide median tooth, and bicuspid major lateral (*op. cit.*: fig. 8).

The examination of about 30 lots of *Oldroydia percrassa* brought out the following points: In color, most specimens are a uniform tan or light brown; however, a few specimens are much lighter, creamy, almost white. In length, many specimens reach 2 cm; the largest specimen examined, preserved in ethyl alcohol, measures 28.0 mm in length (LACM 67-47, Punta Banda, Baja California, Mexico, at 18-22 m). The smallest specimen examined (LACM-AHF 1257-41, Natividad Island, off Baja California, Mexico, at 55-57 m), measures 2.8 mm in length. This juvenile specimen, like other juveniles examined, reveals features quite distinct from adult specimens, and not previously described: In juveniles (1) the shell is relatively light, not thickened at all, (2) the shell is moderately carinated, (3) the valves are beaked, (4) the jugal area is not clearly defined, (5) there is only a suggestion of wrinkles in the

pleural areas, and (6) the girdle does not show encroachment at the sutures. Thus, in *O. percrassa* intra-specific variation is much more accentuated than expected, at least on account of significant changes that take place as the specimen matures and grows in length and thickness. In this respect, it is important to note that particularly the mucro shows considerable variation since it reflects the changing degree of thickness of the posterior valve; in juvenile specimens the postmucro area is definitely concave in profile, instead of the strong convex outline usually seen in old (large) specimens. The differences between juvenile and old specimens in the case of *Oldroydia percrassa* are so pronounced as to easily induce a chiton worker into the belief that they represent two (or more) species. An adult specimen is here illustrated (Figure 20).

The radula of a specimen 27.0 mm long (AJF 246, Santa Cruz Island, California, at 9 m) measures 12.5 mm in length (46% of the specimen's total length), and has 65 rows of mature teeth. In all respects, it conforms well to the account given in THIELE (1910). The median tooth, large in front where it measures about 132 μ m in width; major lateral teeth have a bicuspid head, measuring about 200 μ m in length, 150 μ m in width; outer marginal teeth are 200 μ m long, 120 μ m wide, with a length/width ratio of 1.67.

Distribution: *Oldroydia percrassa* ranges from Monterey Bay, California (36°45'N; 121°45'W) where it has been often collected (CASIZ 008956; CASIZ 008957; CASIZ 008958; AJF 342) to San Benito Island, Baja California Mexico (23°18'10"N; 115°32'20"W) (LACM-AHF 1248, intertidal, February 25, 1941). It has been found, also, in the offshore islands, Catalina (LACM 70-77, LACM-AHF 2049-51, AJF coll.), Santa Cruz (LACM-AHF 1297-41), Santa Rosa (LACM-AHF 41, LACM-AHF 1417-41), Anacapa (LACM-AHF 875-38, LACM-AHF 1270-41), Santa Barbara (LACM-AHF 984-39), Cordell Bank (CASG 53410), San Martin (AJF 95), and Natividad (LACM-AHF 1417-41). It has been found in the Gulf of California, Mexico at Salsipuedes Channel (Scripps Station p-58-59, VSS-62), at 457 m; the specimen, whitish in color measures 18.0 mm in length, 9.0 mm in width; moderately carinated, postmucro slightly concave, the valves somewhat beaked, the jugal area not well demarcated (CASIZ 002382); color slides of the specimen, CASIZ Color Slides Series Nos. 735 and 736.

Oldroydia percrassa has also been reported from the Sea of Japan (JAKOVLEVA, 1952; IWAO TAKI, 1964).

The bathymetric range of *Oldroydia percrassa* extends from the intertidal zone (LACM-AHF 1248-41, San Benito Island, Baja California, Mexico) to 640-731 m (LACM-AHF 2049-51, Catalina Island, California), with a median depth, based on the collections available, of 40 m.

Remarks: The description and illustrations of *Hanleya spicata* Berry, 1919, indicate that the single specimen, 4.5 mm in length, collected off Point Pinos, Monterey Bay, California, at 60 m, is a juvenile of *Oldroydia percrassa*. Berry himself expressed doubts about the specimen's identification, noting that it is "quite likely not mature . . . (and) it may prove to be only a variant of the older species *Hanleya hanleyi* (Bean, 1844) . . . (which) for the first time establishes the genus *Hanleya* in Pacific waters." (BERRY, 1919: 10).

As it appears, now, the genus *Hanleya* Gray, 1857, is not present in Pacific waters, or at least not in the eastern Pacific. The references to *H. hanleyi* in the eastern Pacific (OLDROYD, 1927; SMITH, 1947a, 1947b; SMITH & GORDON, 1948; JAKOVLEVA, 1952) could not be confirmed; they are either presumptive or reflect the misidentification of juvenile specimens of *Oldroydia percrassa*. THIELE (1909: 15) identified a specimen collected at Plover Bay, Bering Sea, as *H. hanleyi*; but JAKOVLEVA (1952) expressed doubts about the presence of *H. hanleyi* in the Bering Sea, although accepting its presence [*? ex* OLDROYD, 1927] in Monterey, California.

A second species of *Oldroydia* has been described from Japan: *O. bidentata* Taki, 1938, based on a single specimen, 45 mm long, collected at 100-140 m in Sagami Bay, Japan.

DISCUSSION

This study shows that a number of erroneous records had crept into the identification of the eastern Pacific lepidopleurids. *Leptochiton alveolus*, thought to be confined to the North Atlantic, is now found to be widely distributed in the eastern, as well as western Pacific. On the other hand, the alleged presence of *Leptochiton cancellatus* and *Hanleya hanleyi* could not be corroborated; both species are to be considered now as confined to the North Atlantic. But a few other nominal species of presumed eastern Pacific lepidopleurids require commentary.

Lepidopleurus (Leptochiton) nicomedes DALL, 1919: 501-502. The holotype (USNM 96935) was examined through the courtesy of Dr. Joseph Rosewater. The labels read: "Coast of Patagonia, South America/sta. 2781, 348 fms., m. 49° 9', off Nelson str./S. Lat. 51° 52', W. Lon. 73° 41'," and "Type." The single specimen (Figures 25, 26, 27) dried, creamy white, curled, has an estimated length of 12 mm, and estimated width (including girdle) of 7 mm. Valves carinated. Lateral areas elevated, well defined, with a faintly nodose surface; the nodosities align themselves in 3-5 poorly defined radial ribs transversally cut by some 12 sulci. Central areas with no obvious sculpture except for a micro-rugose appearance and a very weak tendency to

form longitudinal riblets; these riblets are more accentuated in the pleural areas where they vaguely continue the transverse sulci of the lateral areas. Girdle fully covered with cylindrical scales, neatly imbricated so that only their upper ends show; the girdle scales measure about 100 μ m in height, and 70 μ m in width. A portion of valve vii, denuded of girdle, displays a white articulamentum, and permits the observation of an insertion plate and, at least, one slit. The gills, though difficult to visualize in the dried specimen, are seen to extend forward to about the front edge of valve iii. Obviously, the specimen is not a lepidopleurid. In fact, it is a specimen of *Ischnochiton exaratus* (Sars, 1878), as subsequently confirmed by comparing it with an authentic specimen of *I. exaratus*, collected at Galgenes, Norway, at 200-300 m, and graciously made available to me through the kindness of Dr. P. Kaas, The Hague, The Netherlands. Color slides of *Lepidopleurus nicomedes* Dall, 1919, deposited in the CASIZ Color Slides Series.

Lepidopleurus (Leptochiton) agesilaus DALL, 1919: 501. The syntypes, 2 dry, curled, specimens (USNM 9627), were examined thanks to the generosity of Dr. Joseph Rosewater. The shells are round back, i.e. not carinated. The label reads "Type," and "Sta. 2778, 61 fms., sd. 48°/Sts. Magellan." The tegmentum of both specimens is covered with a black, bituminous material except for the anterior 1/6 of the valves which, in the living animal, would have been covered by the overlapping of the valves in the front. The unblackened portion of the valves is creamy-white and shows the tegmental sculpture of longitudinally arranged granules, coalescing enough to define longitudinal striae, about 30 to 40 per half size. Lateral areas poorly defined, except by the different, radial, direction of the granose striae, and the presence of a few concentric growth wrinkles. Girdle pebbly, with no visible spicules. Mucro central, on a somewhat inflated valve. The estimated length of the animals is 7 and 5 mm. The largest specimen (Figure 28) is here designated as lectotype, and illustrated for the first time. In the original description, DALL (1919) states that "the jugal sinus obsolete, the sutural laminae small and narrow"; unless Dall had more specimens at hand, to which he makes no reference, this is a puzzling statement since neither one of the type specimens had been disarticulated to permit observations about the sinus and the sutural laminae. Dall's statement that the "posterior edge (of the valves) irregular denticulate," is incorrect, for the irregularity of the valves' posterior edge is obviously an artifact, the result of erosion, perhaps related to the black deposits on the shell. There is no evidence, either, of what Dall describes as "obscure concentric undulations," unless he was referring to the growth lines to be seen in the lateral areas, and very vaguely in the anterior valve.

Leptochiton agesilaus is in every respect conchologically indistinguishable from *L. rugatus* of the eastern Pacific,

and *L. cancellatus* of the North Atlantic. As mentioned above, the differential diagnosis between *L. rugatus* and *L. cancellatus* rests on the examination of the radula; so, the final question about *L. agesilaus* may have to remain unresolved until more specimens are available for radula study, a pessimistic prospect for since DALL's report (1919), *L. agesilaus* has been often listed but not collected (BOUDET, 1945: 135; CARCELLES, 1950: 47; CARCELLES & WILLIAMSON, 1951: 243; CASTELLANOS, 1956: 466; LELOUP, 1956: 12). A further study of *L. agesilaus* falls outside the scope of this paper. However, future work will have to take into account, also, the possibility that *L. agesilaus* may be a junior synonym of *Leptochiton medinae* (Plate, 1899), described from the same locality, and which LELOUP (1956: 13-14) regards as one of the most abundant chitons in the Magellan Archipelago. Although I have been unable to obtain specimens of *L. medinae* for a direct comparison with the type of *L. agesilaus*, I am inclined to recommend, albeit on subjective grounds, that the two nominal species be regarded as synonyms until proved otherwise.

Color slides of *Leptochiton agesilaus* are deposited at CASIZ, Color Slides Series.

In the course of this review, type material of 3 other Pacific lepidopleurids, *Leptochiton diomedae* Berry, 1917, *Lepidopleurus rissoi* Nierstrass, 1905, and *Lepidopleurus lineatus*, were examined. The study of these specimens reaffirmed the validity of these species, and conclusively demonstrated that they are not to be considered synonymous to any of the eastern Pacific species recognized in this paper.

Leptochiton diomedae BERRY, 1917: 1-3; pl. 1, figs. 1-3; pl. 2. The holotype (USNM 215625) was examined on a loan arranged through the kindness of Dr. Joseph Rosewater. The labels read, "Japan Seas/sta. 4967 off sh [?] Light/USS Albatross," and "Type/sta. 4967, 244-253 fms./off Shio Misaki Light, Japan/USS Albatross (S.S.B.95)." The specimen (Figures 21 & 22), dried, partly disarticulated, light brown in color, corresponds in every respect to the description and illustrations provided by BERRY (1917). Color slides of the specimen at CASIZ Color Slides Series.

Lepidopleurus rissoi NIERSTRASS, 1905: 6-7; figs. 5, 52-55. The specimen examined on loan through the generosity of Dr. H. E. Coomans (ZMA), is one of the 10 specimens of the species collected in the course of the *Siboga* expedition. Nine of these specimens are in the repository of the Zoological Museum of Amsterdam, with "perhaps one specimen kept by Nierstrass" (Dr. H. E. Coomans, *in litt.*, June 13, 1978). The syntype series comprises specimens from 6 *Siboga* stations, with localities ranging from 3°27.1'N to 10°39'S, and from 119°8.5'W to 131°0.5'W, and from

depths between 216 m to 2053 m. The examined specimen, marked "Type," is accompanied by a Museum (ZMA) label reading, "*Lepidopleurus rissoi* Nierstr./Stat. 126/figured specimen by Schepman/fig. 5," a reference to its illustration in NIERSTRASS (1905). The single specimen is preserved in alcohol, partly disarticulated, with only valves ii to v in place. Estimated length of the specimen, 26 mm; width, 10.5 mm. Color uniform white except for abundant deposits of an orange-brown material. In all respects it conforms well to the description and illustrations given by NIERSTRASS (*op. cit.*). Carinate; lateral areas only slightly raised; central areas with about 28 rows of granules per side; jugal angle about 95°; mucro central, slightly pointed; post-mucro, strongly concave. The specimen (Figures 30, 31 & 32) is here designated as **lectotype**. Color Slides of the specimen at CASIZ Color Slides Series.

Lepidopleurus lineatus NIERSTRASS, 1905: 8; figs. 4, 48-51. The specimen loaned for study through the kindness of Dr. H. E. Coomans (ZMA) is part of the 10 syntypes collected by the *Siboga*. The series was obtained in 4 *Siboga* stations, the localities ranging from 0°34.6'N to 10°39'S, and from 119°W to 123°40'W, and from depths between 450 m to 1301 m. The specimen, marked "Type," is accompanied by a label (ZMA) reading "*Lepidopleurus lineatus* Nierstr./Stat. 297/1 specimen." Preserved in ethyl alcohol, it measures 10.8 mm in length, 6.5 mm in width. Color is a golden yellow throughout. NIERSTRASS (1905) description and illustrations conform well with the specimen at hand. Carinate; inwardly curving riblets, about 12 per side, in central area, continuing onto the lateral areas; posterior; mucro central. The valves seem heavy and thick enough to raise the consideration that, on examination of more material, the species might be allocated to *Lepidopleurus* Risso rather than *Leptochiton* Gray. The specimen (Figures 23 & 24) is here designated as **lectotype**. The other specimens comprising the syntype series are at the Zoologisch Museum of Amsterdam, except for "1 in Brussels [Museum], and 1 kept by Nierstrass" (Dr. H. E. Coomans, *in litt.*, June 13, 1978). Color slides of the lectotype at CASIZ Color Slides Series.

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A Statistical Study of *Cypraea tigris* in the Central Pacific

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(2 Text figures)

INTRODUCTION

THERE HAS BEEN much interest in *Cypraea tigris* Linnaeus, 1758, by both collectors and malacologists because of its large size and its color. In Hawaii, the eastern Pacific limit of its geographical range, *C. tigris* attains a size unequaled anywhere else. This larger size, the wider and straighter aperture, larger and stronger teeth, deeper and broader fossula, and the near absence of a marginal callus were the characteristics used by CATE (1961) to separate the Hawaiian form as a distinct subspecies, *Cypraea tigris schilderiana*. KAY (1961) through shell measurements on *C. tigris* was able to distinguish 3 groups based on size: the large Hawaiian subspecies, a population intermediate in size at Johnston Atoll and a smaller form that occurs throughout the south Pacific. Unfortunately, only 14 specimens were available to KAY (*op. cit.*) from Johnston Atoll, and the 3 size groups were not differentiated statistically. FOIN (1972), using the mean shell lengths of *C. tigris* from Hawaii and localities to the south and west, showed that the gradient in shell size is related to the degree of isolation of a given archipelago.

KAY (1961) suggested that the variation in size exhibited by Hawaiian *Cypraea tigris* may be due to lower surface water temperatures (Bergmann's Rule) or to differences in habitats available to the species in Hawaii. In the Hawaiian Islands, *C. tigris* occurs in relatively deep water, often on a dead coral or basalt substratum (CATE, 1961; KAY, 1961). The high Hawaiian Islands have reefs that differ considerably from those of atolls; in the latter localities *C. tigris* occurs in shallow water areas that also harbor a diverse benthic biota. The inverse relationship of larger shell size to lower surface water temperatures is not clear. KAY (*op. cit.*) noted that 2 *C. tigris* available for study, collected in the Northern Hawaiian chain at Midway Island and Kure Atoll (where the lowest Hawaiian surface water temperatures occur), were small in size and closely resembled the normal south

Pacific form. WILSON & SUMMERS (1966), however, have attributed size clines in *C. friendi* off western Australia to corresponding temperature gradients, and SCHILDER (1961) similarly ascribed size clines in *C. arabica* to surface water temperatures.

The validity of the Hawaiian subspecies has been questioned. CATE (1965: 58) and SCHILDER & SCHILDER (1971: 154) recognized the subspecies but BURGESS (1970) and TAYLOR & WALLS (1975) did not; however, no reasons were given for not accepting the subspecies. DONOHUE (1965, 1971, 1977) confined his taxonomic work on *Cypraea* to the species level, thus avoiding trinomials of *C. tigris*. The lack of quantitative information on morphological characters of *C. tigris* makes any assessment of a subspecies tenuous at best. Most of the previous work has been qualitative and hence is subjective. KAY's (1961) findings have shown some interesting gradients in shell size, and FOIN (1972) through regression analysis has presented evidence suggesting that this gradient in size represents a cline. In the present paper I wish to examine this size gradient with adequate sample sizes and appropriate statistical procedures, which may help to determine objectively if the Hawaiian form of *Cypraea tigris* warrants the status of a subspecies.

MATERIALS AND METHODS

All measurements on shells were made with vernier calipers to the nearest 0.1 millimeter. The characters measured included the shell length, width, and height. To be comparable with KAY's (1961) and FOIN's (1972) findings, the present data were considered statistically in 3 geographical groups, *i. e.*, the Hawaiian Islands with 106 specimens, Johnston Atoll with a sample of 70 specimens I collected in 1970, and measurements made on 75 *Cypraea tigris* from other parts of the tropical Pacific (western region - New Guinea, Borneo, Philippines, Palau, and the Great Barrier Reef with 42 specimens as well as

the central region - Marshall Islands, Tuamotus, Carolines, Guam, Tonga, and Fiji with 33 specimens). Shells used in these measurements were from the Burke Museum, Seattle, Washington, and 3 private Honolulu collections. All measurement data were analyzed, using least squares linear regression, analysis of variance, and Newman-Keuls multiple range tests.

RESULTS

Length frequencies of *Cypraea tigris* were plotted; these data seem to fall into 3 groups on the basis of size and locality of collection (see Figure 1). The Hawaiian Islands harbor the largest shells, Johnston Atoll has *C. tigris* of intermediate size (Group 2) and shells from other

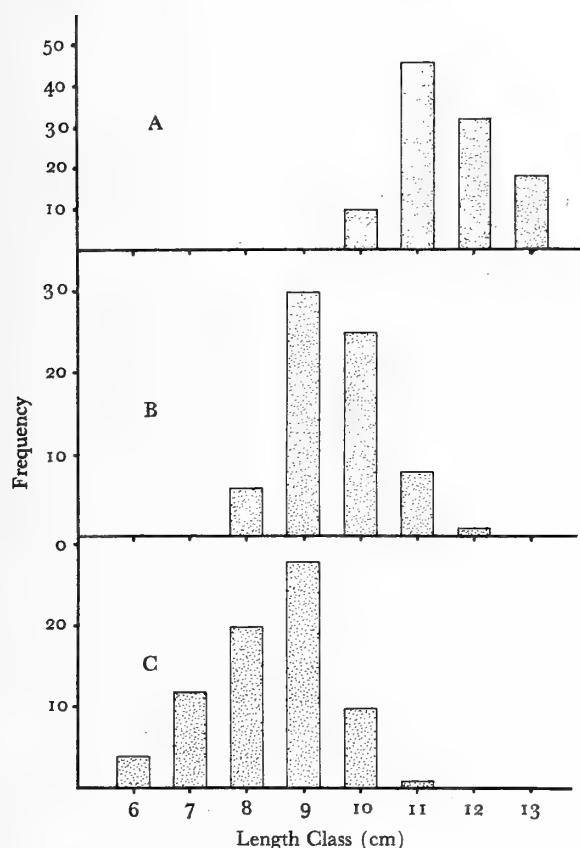


Figure 1

Size frequency plot of the length of *Cypraea tigris* from three geographical areas. The lengths of 106 Hawaiian Island specimens are shown in A, 70 Johnston Atoll specimens in B, and 75 specimens from islands in the Pacific south of Johnston Atoll in C

Pacific Islands are the smallest and make up the third group. These findings agree with those of KAY (1961) and FOIN (1972).

The relationship of the shell length to breadth from the 3 geographical areas was explored to determine if the slopes of a fitted regression of shell length (X) to shell width (Y_w) differed. Table 1 presents a summary of these regressions, and the lines are plotted in Figure 2. The slopes of the plotted lines are very similar and all differ significantly from zero ($P < 0.001$). The slopes do not differ significantly, implying that the shape of adult shell (the length to width relationship) is similar for specimens from the 3 geographical localities. The same result was obtained for a regression analysis of shell length (X) to shell height (Y_h).

Of the 3 morphological characters measured in this study only the shell length shows appreciable differences that may be related to the collection locality. The results of an analysis of variance of shell lengths from 3 treatments (*i.e.*, geographical areas) is given in Table 2. The mean length of shells from each area differed significantly ($P < 0.001$). To delineate further the statistically significant differences in shell lengths in the analysis of variance, a Newman-Keuls multiple range test (ZAR, 1974) was employed. This test compares the mean shell length from one geographical location against another. The results of this test are given in Table 3 and the mean lengths of shells from each locality are significantly different ($P < 0.005$).

DISCUSSION

The results suggest that there are 3 distinct groups of *Cypraea tigris* in the central Pacific based on size. If size alone may be used as a criterion for subspecies differentiation, then the Hawaiian form warrants this separation. The shells from Johnston Atoll are puzzling in that they have all the characters of the Hawaiian form but are intermediate in size. Are they more closely related to the Hawaiian or the south Pacific forms or do they represent yet another subspecies?

Johnston Atoll is isolated, lying 720 km southwest of French Frigate Shoals in the Hawaiian Archipelago, over 2 000 km from the Marshall Islands to the west and 1 100 km from Kingman's Reef in the Line Islands to the south. Biological collections have been made over the years at Johnston by EDMONDSON *et al.* (1925), FOWLER & BALL (1925), WELLS (1954), GOSLINE (1955), BROCK, JONES & HELFRICH (1965), BROCK, VAN HEUKELEM & HELFRICH (1966), BUGGELN & TSUDA (1966), BROCK

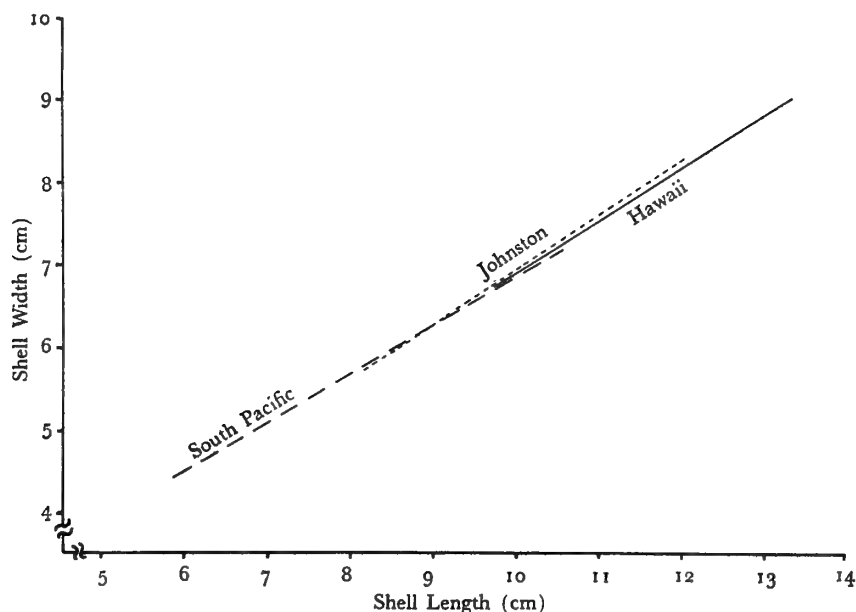


Figure 2

Least squares linear regression of shell length (X) against shell width (Y) for specimens from three geographical areas, *i. e.*, 76 specimens from the South Pacific (dashed lines), 70 specimens from Johnston Atoll (dotted line), and 106 specimens from the Hawaiian Islands (solid line)

Table 1

Results of the linear regression analysis of shell length (X) against shell width (Y_w) in centimeters for specimens from the three localities. Given in the table are sample sizes (N), the calculated regression equations and the coefficients of determination (r^2), a measure of the variation in Y_w (shell width) accounted for by the regression. In all cases the F test indicates that the slopes of the three regression lines differ significantly from zero ($P < 0.001$).

Area	N	Fitted Equation	Coefficient of Determination (r^2)	F
Hawaii	106	$Y_w = 0.68 + 0.63X$	0.80	424.07**
Johnston	70	$Y_w = 0.29 + 0.67X$	0.84	345.14**
South Pacific	75	$Y_w = 0.99 + 0.59X$	0.90	674.86**

(1973), BAILEY-BROCK (1976) and BROCK (1979). These studies suggest that the marine fauna is primarily Hawaiian with only a few central Pacific elements being present. However, the dominant corals at Johnston belong to the

genus *Acropora*. The genus is virtually absent from around the main Hawaiian Islands, and the *Acropora* at Johnston provide habitats that are similar to atolls to the south and west but that differ greatly from those around

Table 2

Table of the analysis of variance of the lengths of *Cypraea tigris* from 3 areas in the Pacific. The large F value indicates that the mean lengths of shells is significantly different amongst the 3 treatments (geographical localities).

Treatments	Number of Observations (N)	Mean Length (cm)	Standard Deviation
Hawaii	106	11.53	0.83
Johnston	70	9.51	0.78
South Pacific	75	8.43	1.05

Summary of the Analysis of Variance:				
Source	Sum of Squares	DF	Mean Square	F
Treatments	447.21	2	223.60	281.89**
Error	196.72	248	0.79	
Total	643.93	250		

Table 3

Results of the Newman-Keuls multiple range test used to analyze the mean length of *Cypraea tigris* shells from 3 geographical locations. In all cases the mean lengths differ significantly from each other ($P < 0.005$).

Comparison of Lengths	Calculated Studentized Range (q)	P	q0.005 DF = 248, P	Conclusion
Hawaii vs S. Pacific	32.55	3	4.42	lengths not equal ($P < 0.005$)
Hawaii vs Johnston	20.78	2	3.97	lengths not equal ($P < 0.005$)
Johnston vs S. Pacific	10.28	2	3.97	lengths not equal ($P < 0.005$)

the high Hawaiian islands. These differences in benthic habitats may be responsible for the intermediate sizes of *Cypraea tigris* at Johnston Atoll.

Johnston Atoll is situated in the northeast tradewind belt and is bathed by the North Equatorial Current. This current passes by the high Hawaiian Islands moving at speeds up to 20 cm/second (SVERDRUP, JOHNSON & FLEMING, 1942) towards Johnston Atoll 1300 to 1400 km to the southwest. This current may serve to carry larval forms of Hawaiian marine invertebrates to Johnston Atoll. BROCK (1973) notes the occurrence of the endemic Hawaiian lobster *Panulirus marginatus* at Johnston and I have collected alive the Hawaiian endemic cowry, *Cypraea tessellata* Swainson, 1822 at Johnston. GOSLINE (1955) has recorded several Hawaiian endemic fish species at Johnston. However, the *C. tigris* population at Johnston is probably not totally dependent on larvae from Hawaii, for on several occasions I have found *C. tigris* pairs brooding eggs at Johnston. This suggests that the population may be self-sustaining.

The only morphological character of *Cypraea tigris* that is readily quantifiable and consistently different in the Hawaiian and Johnston populations is shell size. Other characters used by CATE (1961) in differentiating the Hawaiian subspecies are variable or subjective when one inspects large numbers of specimens. The linear regression analyses indicate that the shape of the adult shell is the same for all populations; hence, the subspecies separation without further experimental evidence must be based only on shell length. Regardless of the statistical evidence, the presence of a population of *C. tigris* intermediate in size at Johnston Atoll suggests that a gradient or cline of size characteristics exists in *C. tigris* from the south Pacific population through Johnston Atoll to the Hawaiian Islands. These findings agree with those of FOIN (1972). SCHILDER (1969) has noted that the size of many cowry species increases towards the periphery of their ranges, producing a cline in size.

The different habitat occupied by the large *Cypraea tigris* of Hawaii and the presence of an intermediate

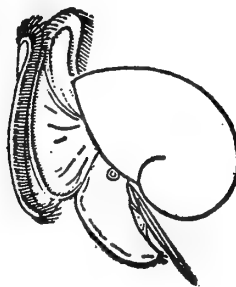
sized form at Johnston Atoll in shallow-water habitats similar to those occupied by the species further south, suggests that this species simply exhibits a gradient in shell size that may be related to differences in environmental conditions. *Cypraea tigris* probably has a phenotypic plasticity that is manifested by morphological (size) variations in response to varying ecological conditions. Thus, as concluded by FOIN (1972), the validity of the Hawaiian subspecies is doubtful and until further experimental work is done, the trinomial should not be used.

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Pholadomya candida Sowerby: The Last Cadaver Unearthed

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

A FEW LIVE SPECIMENS of the deep-burrowing bivalve *Pholadomya candida* were collected in the Virgin Islands during the last century, but the species now appears to be extinct (RUNNEGAR, 1972). I had previously attempted unsuccessfully to locate a preserved animal in the wet collections of European and North American museums. In 1975, Mrs Solene Whybrow, British Museum (Natural History), wrote to say that she knew of a single specimen in the Universitetets Zoologiske Museum, Copenhagen; through the courtesy of Dr J. Knudsen, I was able to examine this specimen in Copenhagen in July 1977.

In 1972 I attempted to reconstruct the anatomy of *Pholadomya candida* by combining information contained in an old (ca 1840) unpublished manuscript by Richard Owen with observations made from the shells. Most of the shell features were explained by Owen's anatomical

notes but it was difficult to interpret 3 accessory muscle insertions associated with the anterior end of the pallial line on each valve (Figure 1, j-l). Two pairs of these (Figure 1, k & l) are now known to be the insertions of a unique anterior 'cruciform' muscle system which seems to have been used to manipulate the position of a small pedal orifice in the otherwise almost completely sealed ventral mantle lobes. It is suggested here that this orifice could be positioned by the muscles to direct water jets from the mantle cavity into the substrate. The erosive action of the water jets probably enabled *Pholadomya candida* to increase the depth of its burrow. This specialized adaptation apparently replaced the function of the foot, which is atrophied in the adult animal. Its fire-hose like action may be convergent with or ancestral to the method of burrowing possibly used by some of the related 'watering-pot clams' of the family Clavagellidae. In any case, it probably made *P. candida* particularly vulnerable to habitat disturbance and hence extinction. The appearance of muscle insertions of the 'cruciform apparatus' in Early Tertiary species of *Pholadomya* can probably be correlated with the virtual disappearance of *Pholadomya* from the late Cenozoic fossil record (ZINSMEISTER, 1978).

New Information on the Anatomy of *Pholadomya candida*

A fine specimen of *Pholadomya candida* collected on August 5, 1838, at St Thomas, Virgin Islands, is preserved in alcohol in the Universitetets Zoologiske Museum in Copenhagen. The shell is articulated and the ligament preserved (Figure 2). The animal has been separated from the shell and the mantle lobes cut open (Figure 4). No attempt was made to dissect the animal since it is unique; this could be done in future by an experienced anatomist.

Little can be added to Owen's description of the anatomical features of *Pholadomya candida* (reproduced in RUNNEGAR, 1972), except that it is now possible to under-

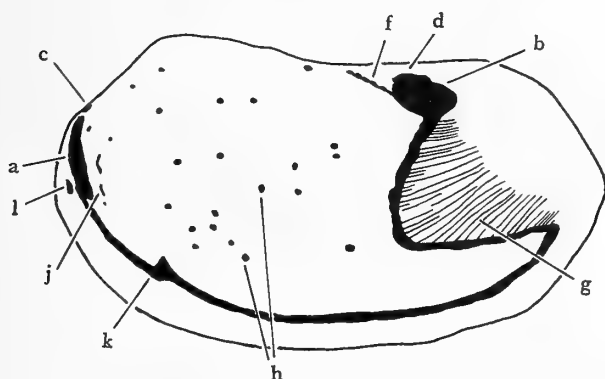


Figure 1

Muscle insertions (black) on left valve of *Pholadomya candida*

- | | |
|---|--------------------------------|
| a - anterior adductor | b - posterior adductor |
| c-d - pedal retractors | f - gill suspensors |
| g - impressions of hypertrophied radial siphonal retractors | |
| h - mantle attachment scars | j - muscle of unknown function |
| k-l - muscle insertions of anterior 'cruciform apparatus' | |

From RUNNEGAR (1972: fig. 1)

stand fully his description of part of the anterior accessory pallial musculature: 'Two bands of muscle fibres, half an inch long, diverge from behind the anterior adductor and terminate in the external edge of the ventromarginal muscles of the mantle.'

The posterior parts of these muscles (Figure 4) are inserted in each valve within the pallial line (site k, Figure 1). These insertions are behind the small pedal orifice (Figure 4). The muscles run anteriorly, cross beneath the anterior adductor, and are inserted outside the pallial line near the bases of the anterior adductor muscle insertions (Figure 3; site l, Figure 1). Although it is difficult to demonstrate this in the preserved specimen, it seems likely that alternate contractions of the anterior and posterior parts of the 'cruciform apparatus' could have served to move the position of the pedal orifice with respect to the shell. The muscles are attached to the mantle at the point where they cross beneath the foot.

DISCUSSION

The foot of *Pholadomya candida* is very small (RUNNEGAR, 1972) and the pedal orifice is so short (Figure 4) that it is difficult to imagine that the animal could have burrowed in the normal way. While it is most likely that *P. candida* would have occupied a single burrow for the whole of its life, it probably would have needed to deepen the burrow as the animal grew. I suggest that it did so by squirting water out of its pedal orifice. This water jet could have been produced by the animal simultaneously adducting the valves and withdrawing the siphons. The jet may have been directed by movements of the muscles of the 'cruciform apparatus' described above.

The only observations that have been made of living bivalves of the extraordinary family Clavagellidae are those of PURCHON (1956, 1960) on *Brechites penis* Linnaeus. In the second article, PURCHON suggested that *B. penis* burrows by squirting water out of holes in its perforated anterior disk. It apparently does so by using regular movements of a thick muscular pallial septum

which limits the mantle cavity anteriorly. Although this method of burrowing has probably developed convergently in *Pholadomya* and the Clavagellidae, it is interesting to note that both are related members of the subclass Anomalodesmata.

The only fossil specimen of *Pholadomya* I have seen which shows any trace of the mantle insertions of the 'cruciform apparatus' is *P. virgulosa* Sowerby from the Eocene London Clay (RUNNEGAR, 1972: 53). If the appearance of this structure is to be correlated with the reduction in size of the foot, and if the animals abandoned the conventional method of burrowing in the Early Tertiary, this would explain the decline in abundance of *Pholadomya* seen in younger Cenozoic rocks. As ZINSMEISTER (1978) has rightly observed, *P. candida* is probably the only Holocene species of *Pholadomya*; other species previously placed in the genus should be referred to *Panacca* Dall, 1905 or other genera. It is therefore disappointing that this nineteenth century endangered species of a genus with such a long fossil record has so recently become extinct.

NOTE ADDED IN PROOF

Since this article was submitted for publication I have learned that Dr. B. Morton, Department of Zoology, University of Hong Kong, has been sent the specimen for detailed anatomical study. His work should be ready for publication in the near future.

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Explanation of Figures 2 to 4

Preserved specimen of *Pholadomya candida*

Figure 2: Dorsal view of specimen in shell; note intact ligament

× 1.5

Figure 3: Ventral view of animal showing small pedal orifice, the ends of the anterior adductor muscle, and the anterior ends of the 'cruciform apparatus' (left muscle arrowed) × 2

Figure 4: Right lateral view of whole animal × 2
Note the posterior parts of the 'cruciform apparatus' (right muscle arrowed) passing beneath the anterior adductor



Figure 2



Figure 3

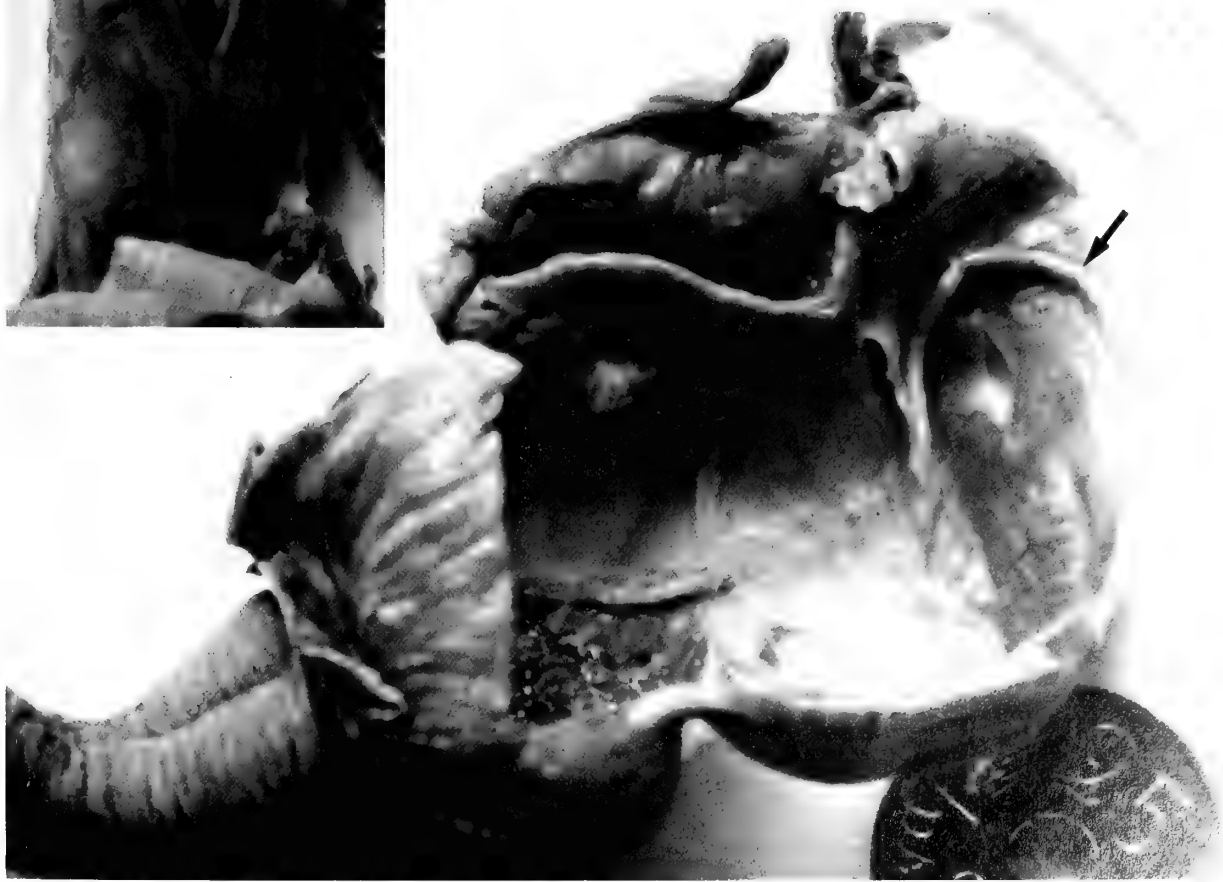


Figure 4

The Ultrastructure and Evolutionary Significance of the Ocelli in the Larva of *Katharina tunicata*

(Mollusca : Polyplacophora)

BY

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(3 Plates; 2 Text figures)

INTRODUCTION

IN A PREVIOUS REPORT we described the ultrastructure of the cerebral ocelli in *Mytilus edulis*, a bivalve mollusk, and noted that, as distinguished from "eyes" in general, the cerebral ocelli of protostomous coelomates studied to date share several features, including rhabdomeric photoreceptors (ROSEN *et al.*, 1978). We concluded these similarities to be the result of evolutionary homology rather than of convergent evolution, although opinions in this matter vary (cf. SALVINI-PLAWEN & MAYR, 1977).

Among the molluscan classes that bear them, the cerebral ocelli of Polyplacophora have remained to be investigated at an ultrastructural level. Because information bearing on this primitive group would aid in clarifying the evolutionary relationships among the cerebral ocelli of protostomous coelomates, we here describe and evaluate the ultrastructure of ocelli in the larva of the black chiton *Katharina tunicata* (Wood, 1815).

The present description relates to the structure of ocelli in the trochophore larva since, unlike the cerebral ocelli of gastropods and a few bivalves, those of chitons generally do not persist long after metamorphosis.

MATERIALS AND METHODS

Katharina tunicata is common to the upper rocky intertidal region of the West Coast of temperate North America. Living, cultured trochophore larvae of this species, electron microscopical supplies, and laboratory space were provided the senior author during June, 1977, at the Friday Harbor Laboratories, University of Washington, through the courtesy of Dr. Dale B. Bonar (pres-

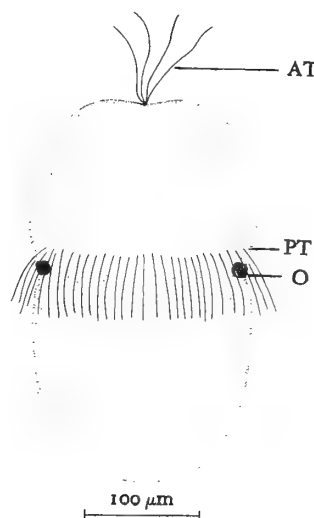


Figure 1

Dorsal view of 160 hour trochophore larva of *Katharina tunicata* (from a preserved specimen)

[for explanation of abbreviations see foldout at end of article]

ent address: Department of Zoology, University of Maryland, College Park, MD 20742).

Specimens 160 and 250 hours old were prepared according to the procedures described by ROSEN *et al.* (1978) for subsequent light and electron microscopical examination at Sonoma State University.

OBSERVATIONS

The trochophore larvae used in this study varied little in size, averaging $350\ \mu\text{m}$ in length and $150\ \mu\text{m}$ in diameter (Figure 1). Slightly anterior to the mid-point of its anteroposterior axis, each larva is encircled by a prototrochal ring of cilia (Figure 1, PT). In living specimens, the ocelli appear as a conspicuous, bilateral pair of red spots situated somewhat posterior to the prototroch (Figures 1, 2, 3, O).

Each ocellus is ovoid and averages 18 by $26\ \mu\text{m}$. Its most obvious feature under the light microscope is an aggregation of pigment granules within the pigment cells (Figures 4, 5, PC). These cells collectively form a hemispheric cup, the space within being the ocellar cavity (Figures 4, 5, OC). At, or near the base of the ocellus, a single sensory cell projects through the pigment cup into the ocellar cavity (Figures 4, 5, SC).

The ocellar cavity may open through an ocellar aperture (Figure 4, OA) into the surrounding medium, or the ocellus may lie slightly below the surface of the epithelium and lack an orifice to the outside (Figure 5). In all instances, the ocellus lies within the epidermal epithelium of the larva. The cells of the ocellus and the adjacent epithelium are separated from the underlying tissues by a basal lamina (Figures 6, 8, BL). Large lipid droplets, representing larval yolk reserves, are found in all the cells at this stage in the development of these larvae (Figures 4-6, 8, LD).

ULTRASTRUCTURE

Sensory Cell: The single sensory cell is somewhat dumb-bell-shaped, being much broader at the proximal and distal ends than in the mid-region (Figures 6, 8, SC). The overall length of this cell, including apical microvilli, is about $25\ \mu\text{m}$. The proximal end is the broadest region of the sensory cell. Averaging $9\ \mu\text{m}$ wide, it contains a number of organelles and the nucleus, which is oval and slightly less electron-dense than the nuclei of the pigment cells (Figures 6, 8, SN, PN). Mitochondria and membrane-bounded cytoplasmic vesicles are the

most numerous constituents of the proximal cytoplasm (Figures 6, 8, M, CV). The vesicles range from 60 to $120\ \text{nm}$ in diameter. Glycogen granules, microtubules, and a few pigment granules were also observed in this region. Axonal extensions of the sensory cell are presumed to exist, but they have not been demonstrated in our material.

The mid-region of the sensory cell narrows to an average breadth of $2\ \mu\text{m}$ and contains dense accumulations of cytoplasmic vesicles (Figure 6, CV). Mitochondria and microtubules are also found in this part of the cell.

The distal end of the sensory cell expands and, from an irregular surface about $6\ \mu\text{m}$ across, gives rise to a disorderly array of microvilli (Figures 6, 7, 8, MV, arrows). The diameters of the microvilli are fairly consistent, about $100\ \text{nm}$, and the cores are non-granular and uniformly dense. A cilium with a 9 plus 2 arrangement of microtubules in the axoneme originates from a pit in the apical surface of the sensory cell (Figures 7, 8, C). A circumciliary space (Figure 7, CC) clearly demarcates ciliary and microvillar surfaces.

Pigment Cells: Each ocellus contains approximately 8 elongate pigment cells about $24\ \mu\text{m}$ long by $4\ \mu\text{m}$ wide (Figures 6, 7, PC). The nuclei are oblong in longitudinal section and have a staining density similar to that of epithelial cell nuclei (Figure 6, PN, EN). Mitochondria, lamellar reticula, and cytoplasmic vesicles occur in the nuclear region (Figure 6, M, LR, CV), but in fewer numbers than in the sensory cell.

Distal to their nuclei and extending to the cell apices, the pigment cells contain accumulations of electron-dense granules (Figures 6, 7, PG). In most instances the granules are bounded by membranes, but such membranes are not always discernable. The granules average slightly less than $1\ \mu\text{m}$ in diameter and are probably not melanin, as judged from the red color of the ocelli in living specimens. Microtubules, lysosome-like organelles, and a few cytoplasmic vesicles also characterize this region of the pigment cell.

At their apices the pigment cells bear microvilli that are about $\frac{1}{4}$ the length and more regularly organized than those of the sensory cell. Cilia have not been observed

Explanation of Figures 2 to 5

Figure 2: Parasagittal section of entire larva showing post-trochal location of an ocellus $\times 450$
Figure 3: Cross section of entire larva $\times 450$

Figure 4: Ocellus in transverse section $\times 1000$
Figure 5: Ocellus in transverse section $\times 1000$
[for explanation of abbreviations see foldout at end of article]

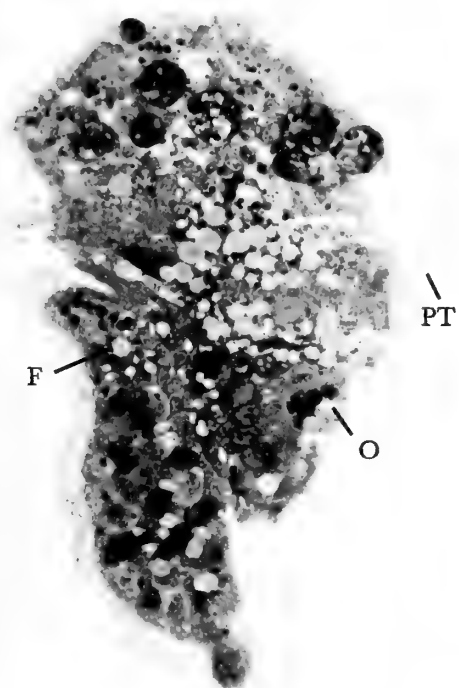


Figure 2

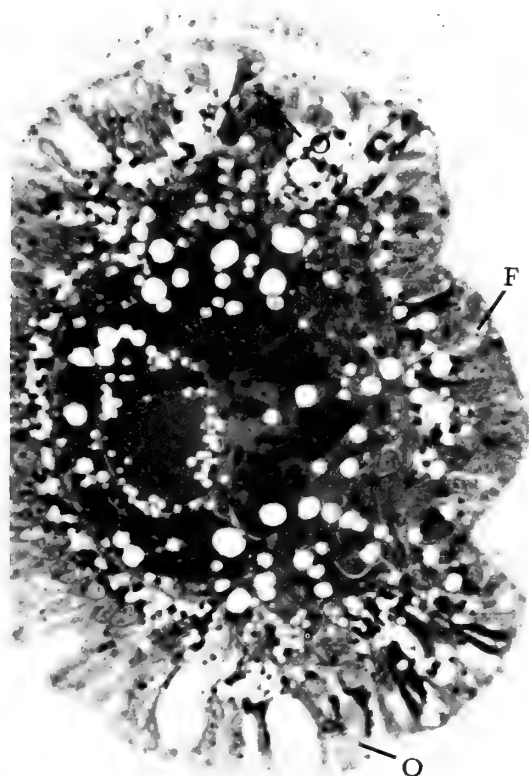


Figure 3

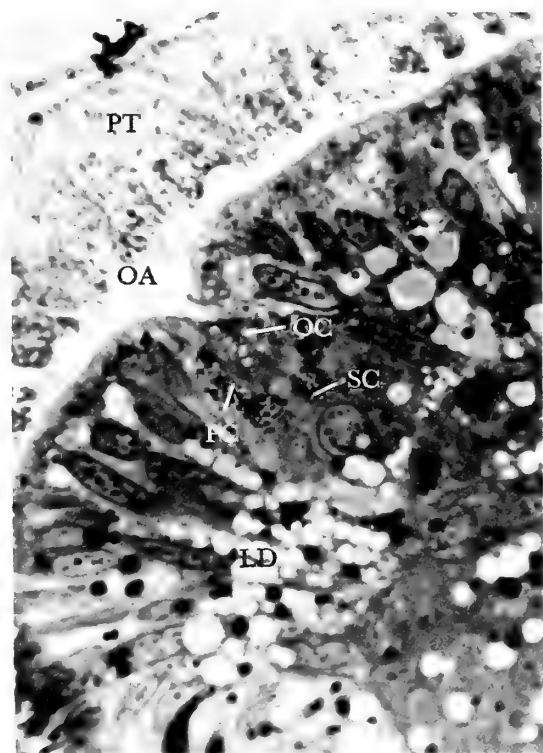


Figure 4

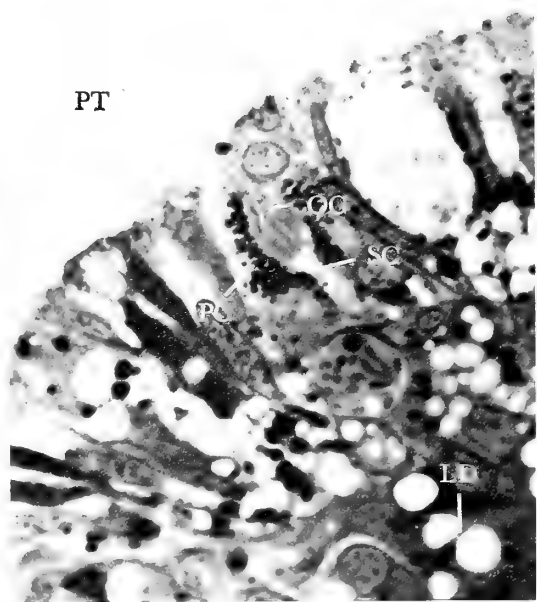


Figure 5

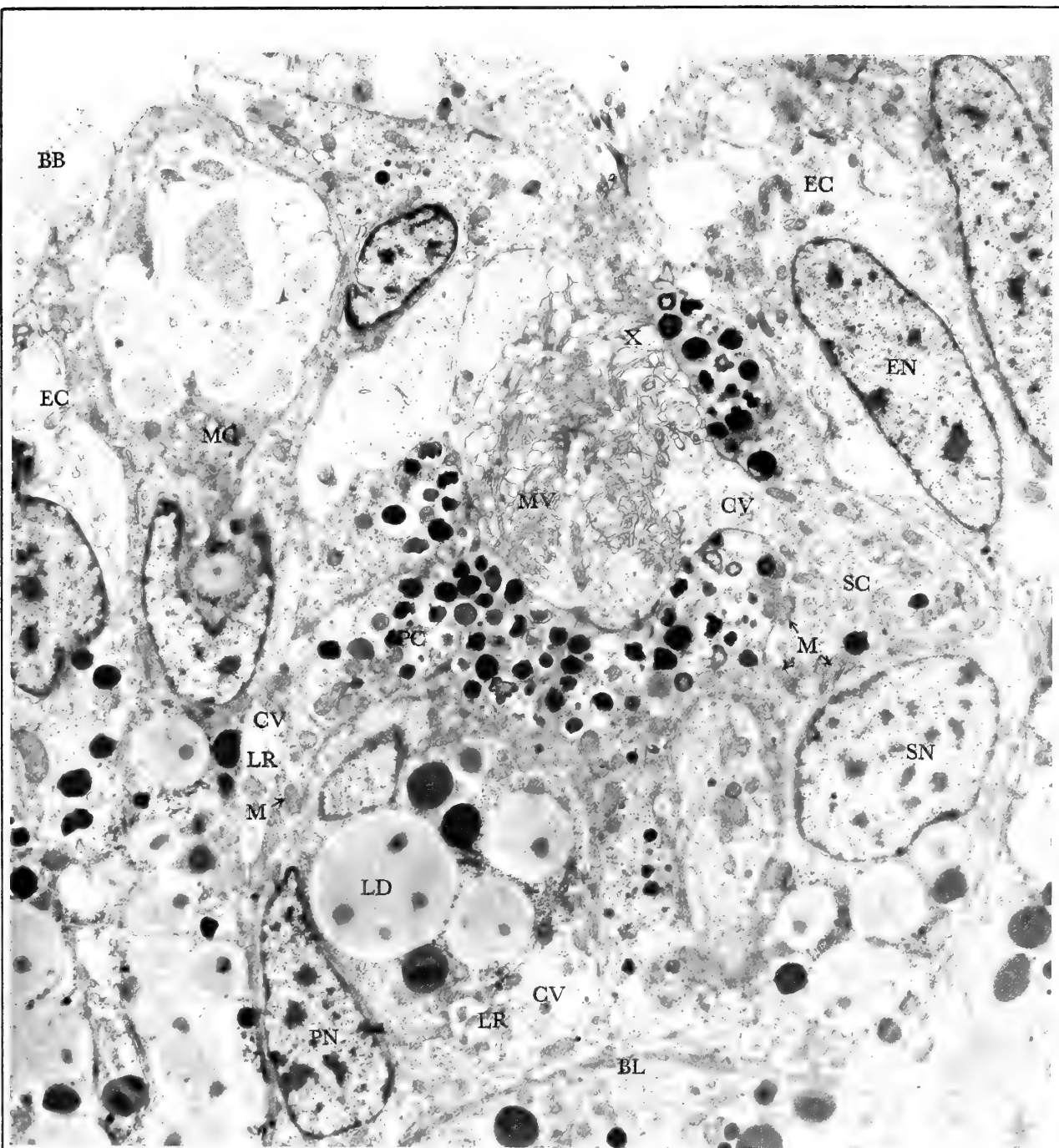


Figure 6

Figure 6: Ocellus in transverse section $\times 5100$
 [for explanation of abbreviations see foldout at end of article]

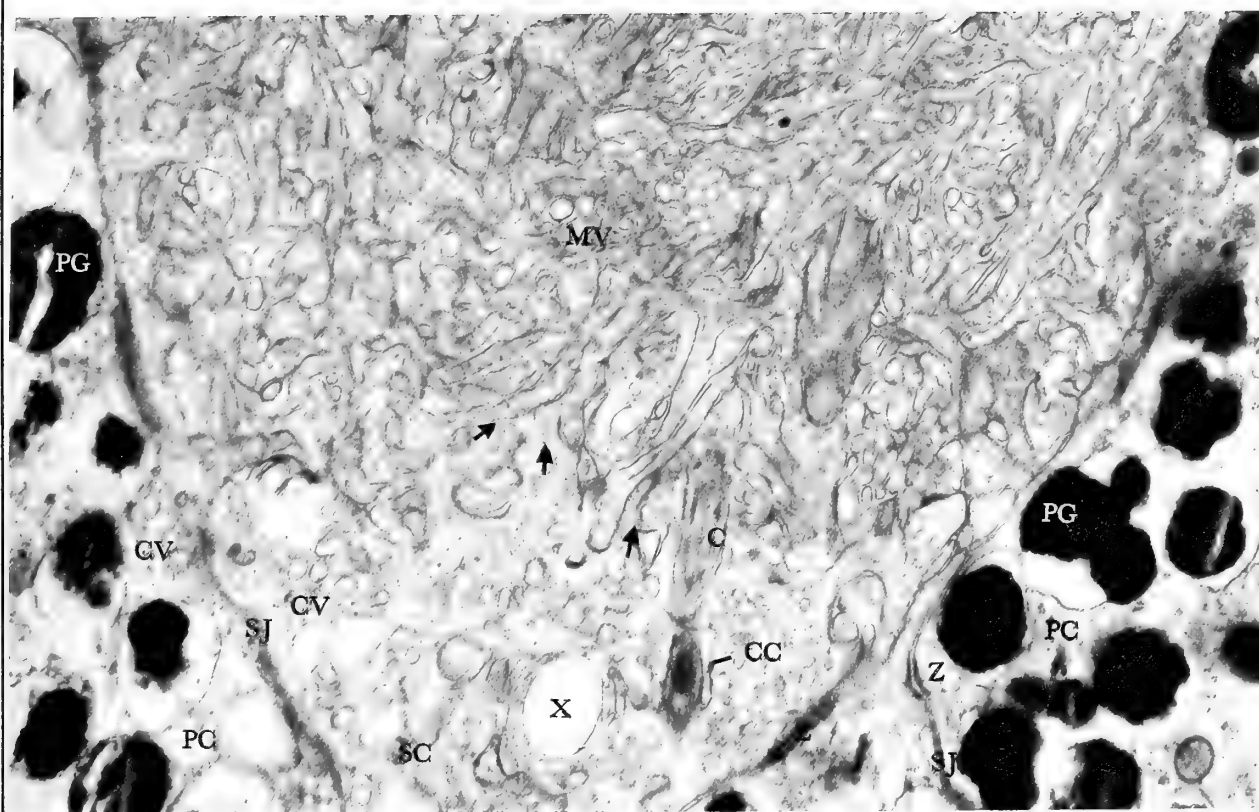


Figure 7

Figure 7: Apex of Sensory Cell $\times 21\,000$
arrows - origins of microvilli from cell apex
[for explanation of abbreviations see foldout at end of article]

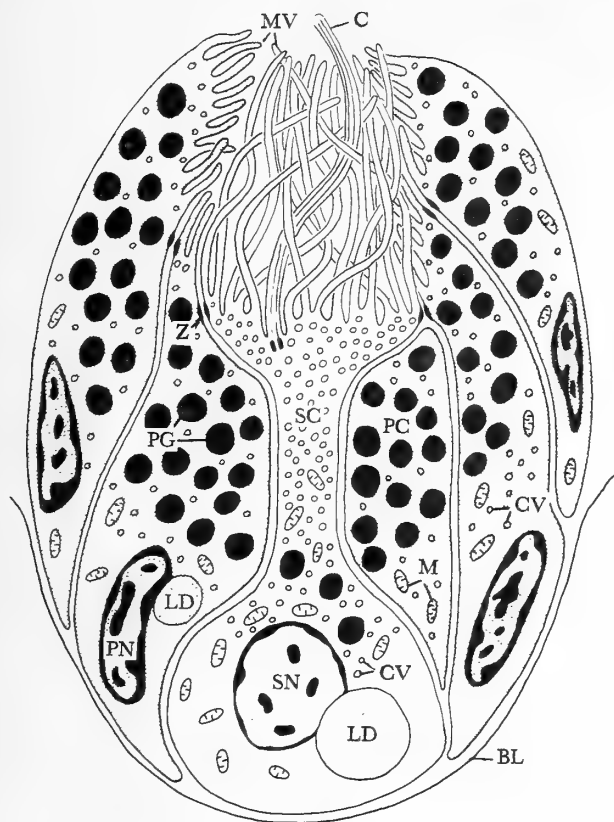


Figure 8

Reconstruction of Ocellus in Section

[for explanation of abbreviations see foldout at end of article]

to originate from the pigment cells. Adjacent apices display adhering zonules and septate junctions (Figures 7, 8, Z, SJ).

Other Features: The cells comprising the columnar epithelium adjacent to the ocellus are about $20\text{ }\mu\text{m}$ tall and $4\text{ }\mu\text{m}$ wide (Figure 6, EC). The cytoplasm of each contains scattered mitochondria and other organelles. The cell apices give rise to brush borders of stubby microvilli more sparse than those of the pigment cells (Figure 6, BB). Within the epithelial layer, mucous glands have been observed near the ocellus (Figure 6, MG).

DISCUSSION

Structure: An account of the structure of larval ocelli in several species of chitons, including *Katharina tuni-*

cata, was given by HEATH (1904), who described each ocellus as a single pigmented cell surrounding a clear central body. The present investigation reveals, however, that the larval ocellus of *K. tunicata* consists of about 8 pigmented cells and a single sensory cell. What appeared to Heath by light microscopy as a clear central region is actually a mass of rhabdomeric microvilli extending from the apex of the sensory cell (Figure 7).

Heath observed that the ocellus may be sunken somewhat below the surface of the epithelium. Our observations are consistent with those of Heath: an ocellar aperture may or may not open to the surface of the epithelium (Figures 4, 5).

The larval ocelli of *Chiton polii* differ from those of other chitons. They persist to the adult stage and lie at the base of a specialized epithelium that may function as a lens (KOWALEVSKY, 1883; HEATH, 1904; see HYMAN, 1967: 122). The ocelli of this species may be sufficiently developed to be sensitive to precise direction of illumination, or perhaps even be capable of image formation. This is not probable in *Katharina*. The concavity of the pigment cup suggests, however, that the ocellus can provide some directional sensitivity.

The following probable functions of the sensory and pigment cells have been interpreted from their distinctive forms. The sensory cell is characterized by an irregular array of relatively long microvilli, a concentration of organelles greater than that in the pigment cells, and only a few pigment granules. These features implicate this cell with photoreception. In contrast, the pigment cells bear relatively short microvilli, have fewer organelles, and contain smaller nuclei than the sensory cell. A heavy scattering of dense pigment granules is the most distinctive feature of the pigment cells. Thus, they appear to provide a screening layer that allows directionally selective illumination of the photoreceptor component of the sensory cell.

Functional interpretations based upon cell form have been corroborated by electrophysiological evidence from the cerebral ocelli of the nudibranch gastropod *Hermisenda crassicornis*. Cells interpreted on morphological grounds to be sensory produced electropotential changes upon illumination, whereas those interpreted as pigment cells did not (EAKIN *et al.*, 1967; DENNIS, 1967). The ultrastructural similarities among the ocelli of *Hermisenda*, *Katharina*, and other protostomes, indicate that the interpretations of cellular functions offered by EAKIN *et al.* (*op. cit.*) and DENNIS (*op. cit.*) may be extended.

The cilium projecting from the ocellus of *Katharina* originates in a manner similar to that of the sipunculan *Phascolosoma agassizii* (HERMANS & EAKIN, 1975). In both species, the cilium extends from a pit at the apex of

the sensory cell, has a 9 plus 2 arrangement of microtubules in the axoneme, and bears an unadorned plasma membrane. Unlike well-known ciliary photoreceptors, the surface area of the plasma membrane of the cilium is no greater than that of a typical kinocilium.

Evolutionary Significance: The ultrastructure of the *Katharina* larval ocellus is probably characteristic for the class Polyplacophora. HEATH (1904) and KOWALEVSKY (1883) showed that larval ocelli in several species, including *K. tunicata*, are uniform in their structure and location. They were described as small pigment cups with clear interiors located within the larval epidermis immediately behind the prototroch, and placed upon the lateral, or branchial, nerves. These ocelli appear 24 hours prior to the free-swimming stage and persist through settlement and metamorphosis of the larva. HEATH (*op. cit.*) stated that in the young, benthic chitons each larval ocellus lies upon the lateral nerve within the pallial groove and that it remains as long as the shell and mantle are sufficiently transparent to allow light to penetrate, that is until a length of about 5 mm is reached. By this time some small species are already sexually mature. Thus the characteristic larval eyes of chitons are not mere larval structures, for they may persist into adulthood in small, transparent species.

This pair of ocelli is entirely distinct from the eyes found in the shells of certain adult chitons. In these evolutionarily advanced polyplacophorans photoreception occurs by means of numerous structures embedded in the dorsal, or tegmental, layer of the 8 shell plates (OMELICH, 1967; BOYLE, 1969a, b). Each tegmental eye has a transparent, biconvex lens that covers a cup-shaped lacuna or pocket lined by retinula cells which bear well-ordered arrays of microvilli forming a rhabdom in the center of the lacuna. Although there are cilia among these microvilli, Boyle concluded that these were not the origin of the microvilli. Thus these photoreceptors may be classified as rhabdomeric. At the bases of the retinular cells, however, next to the walls of the lacunae, Boyle found whorls of numerous profiles, or lamellate bodies, that originated from cilia. BOYLE (1969b) pointed out that, although these bodies have not been certainly identified as sensory structures, they are very similar to those found in photosensitive structures on the mantles of bivalves, where both ciliary and rhabdomeric photoreceptors have been demonstrated. BOYLE (1969b) stated that the fossil history of the chitons separates them at an early date from the other molluscan classes and suggested that the common features of photoreceptors have evolved more than once. Thus, these tegmental eyes are strictly poly-

placophoran, occurring as specializations within members of a few advanced families. They seem to have replaced the so-called larval ocelli as the functional adult photoreceptor organs.

In our previous paper (ROSEN *et al.*, 1978) we concluded that the structural similarities between the cerebral ocelli of the bivalve *Mytilus edulis* and the cerebral ocelli of other protostomous coelomates may be the result of homology. We also concluded that, because of their different embryonic origins and distinctive ultrastructures, the pallial ocelli found on the mantle edges of certain bivalves probably evolved independently, originating subsequent to the divergence of the bivalves from the other molluscan groups.

Now we bring up the question of whether the larval ocelli of chitons, like the cerebral ocelli of *Mytilus*, may be homologous with the cerebral ocelli of other protostomous coelomates. HEATH (1904) observed that the ocelli of chiton trochophores are essentially like those of annelids, except for the fact that in annelids they develop within the epidermis anterior to the prototroch and are innervated directly from the developing cerebral ganglia, while in chitons they originate immediately posttrochally, situated upon and innervated by the pallial cords connecting the cerebral part of the nervous system with the two sides of the larva. HEATH (*op. cit.*) argued that the structural characteristics of the chiton, as they appeared in phylogenetic development, would have favored a gradual backward shift in the position of ocelli from in front of the prototroch to their present posttrochal location. HEATH (*op. cit.*) concluded that the theory that chiton and annelid eyes are homologous rests on identity of structure.

We now know much more than Heath about the structure of cerebral ocelli in protostomous coelomates and have noted that when one compares these ocelli with other known photoreceptor organs, which for various reasons can be judged not to be homologous, homology seems to be the simplest explanation for the similarities among the cerebral ocelli of protostomous coelomates. This conclusion was substantiated further by the observations of EAKIN *et al.* (1977) that the cerebral ocelli in 4 separate families of archiannelid polychaetes contain rhabdomeric photoreceptors and other structural similarities. Depending upon the view one holds regarding the phylogenetic relationships among archiannelids and other forms, the simple ocelli of the former either make good models for primitive, ancestral cerebral ocelli, or they illustrate structural simplicity in relation to small body size.

Except for some anterior system of the polyplacophora ganglionation. The nerve cell the lengths of the longitudinal (1967). This condition is regarded drawn together into ganglia and into larger masses are regarded gastropods and cephalopods. (nerve cords in chitons reflect nature of the nervous system regard these ocelli of chitons nature.

Both rhabdomeric and ciliary eyes are found in annelids and mollusks. In annelids, mollusks, sipunculan annelids, and arthropods, as distinct from oth-

Principally because eyes are absent in Recent Aplousophora, Monoplousophora, and Scaphopoda, SALVINI-PLAVON & MAYR (1977: 240) stated that the Mollusca were originally eyeless. Accordingly, the cerebral ocelli of the mollusks would have arisen independently, and the rhabdomeric photoreceptors in both annelids and mollusks would represent evolutionary convergence. The absence of cerebral ocelli in Recent Aplousophora, Monoplousophora, and Scaphopoda, however, can be accounted for by the fact that all Recent representatives of these 3 groups are burrowers or live at aphotic depths. The Mollusca probably did not originate as burrowers or at aphotic depths, and it is likely that the ancestral mollusks had cerebral ocelli. The similarities between the cerebral eyes of mollusks and annelids seem to us to support this interpretation.

Two anatomical features of polyplacophoran ocelli appear to conflict with the view that they are homologous with the cerebral ocelli of gastropods and annelids. First, the ocelli originate posterior to the prototroch in chitons (and in bivalves), but typically anterior to it in gastropods and annelids. Second, the ocelli of chitons are innervated from the lateral nerve cords rather than directly from the cerebral ganglia as in the other groups. In spite of these discrepancies, HEATH (1899, 1904) decided that the ocelli of the trochophores of chitons and annelids are homologous. In contrast, PELSENER (1899, 1908) held that positional differences with respect to the prototroch ruled against homology. The variable pre- or post-trochal positions of larval ocelli in opisthobranch gastropods (BONAR, 1976) suggest that the prototroch is not necessarily a reliable reference by which ocellar homology may be definitely excluded.

Except for some anterior enlargement, the nervous system of the polyplacophoran is noted for its lack of ganglionation. The nerve cell bodies are scattered along the lengths of the longitudinal nerve cords (see HYMAN, 1967). This condition is regarded as primitive. Nerve cells drawn together into ganglia and condensation of ganglia into larger masses are regarded as advanced traits in gastropods and cephalopods. Connection of the ocelli to nerve cords in chitons reflects the relatively diffuse nature of the nervous system in this class. Thus, we regard these ocelli of chitons as essentially cerebral in nature.

Both rhabdomeric and ciliary photoreceptors have been found in annelids and mollusks. The cerebral ocelli of all annelids, mollusks, sipunculans, onychophorans, and arthropods, as distinct from other photoreceptor organs

that have been studied to date, contain only rhabdomeric photoreceptors. Opinion will undoubtedly vary as to the significance of this fact. Our view is that the similarities among the more complex cerebral ocelli in these groups are due to their evolution from simple cerebral ocelli in the common stem group. We further believe that the distinction between ciliary and rhabdomeric photoreceptors has meaning in an evolutionary context: that they represent distinct types of photoreceptors that are not readily interconvertible. Ocelli apparently originate when and where they are needed and are lost where they are not, but once evolved they subsequently retain a basic structural configuration that can be recognized in descendant forms.

SUMMARY

The trochophore larva of the black chiton *Katharina tunicata* bears a pair of ocelli, each consisting of about 8 pigment cells and one sensory cell. The latter terminates in a rhabdomeric photoreceptor. This fact supports the theory that the photoreceptors in the cerebral ocelli of annelids and mollusks are evolutionarily conservative features and provides evidence for homology between these ocelli.

The post-trochal position of polyplacophoran ocelli and their location on the lateral nerve cords are not inconsistent with the conclusion that they are homologous with cerebral ocelli originating pre-trochally in other mollusks and annelids.

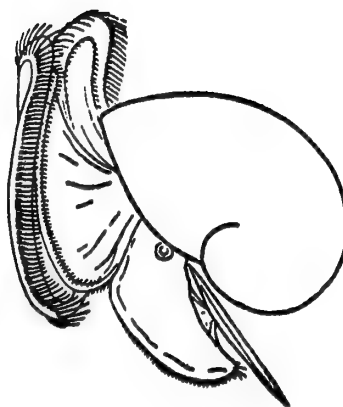
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Explanation of abbreviations

AT - apical tuft	BB - brush border	BL - basal lamina
C - cilium		CC - circumciliary space
CV - cytoplasmic vesicles		EC - epithelial cell
EN - epithelial cell nucleus	F - foot	LD - lipid droplets
LR - lamellar reticula		M - mitochondria
MG - mucous gland	MV - microvilli	O - ocellus
OA - ocellar aperture		OC - ocellar cavity
PC - pigment cell		PG - pigment granules
PN - pigment cell nucleus		PT - prototroch
SC - sensory cell		SJ - septate junction
SN - sensory cell nucleus	X - artifact	Z - adhering zonule

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New Information Concerning *Humboldtiana taylori* Drake, 1951

(Gastropoda : Pulmonata : Helminthoglyptidae)

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

Humboldtiana taylori Drake, 1951, is a species of land snail known heretofore only from a few shells collected at an archaeological site. DRAKE wrote (1951: 94) concerning the type locality: "It was collected dead by Walter W. Taylor, in October of 1947, from the surface of cultural deposits of site C96, northern Coahuila, Mexico. C96 ... is in Media Luna Canyon, in the Fronteriza Range (Serranías del Burro), 16 miles south of Boquillas." Drake's description of the locality is inconsistent. Although both mountain ranges mentioned are in northern Coahuila, the range called Serranías del Burro is located 80-90 km to the east of the Fronteriza Range. (Fossil shells of probable Pleistocene age of *Humboldtiana* have been found in the Serranías del Burro, as noted hereafter).

Dr. Walter W. Taylor confirms (personal communication, 11 October 1976) that the type locality of *Humboldtiana taylori* is in the Fronteriza Range, noting: "Media Luna Canyon is ... northeast of two named places, Jaboncillas and El Melon" The Fronteriza Range comprises the more northern Sierra Jardín and more southern Sierra Maderas del Carmen. El Melón and an Ejido Jaboncillos are shown to the west of the Sierra Maderas del Carmen on the 1:250,000 La Morita Quadrangle (Comisión de Estudios del Territorio Nacional, Joint Operations Graphic Map, Reprint of 1976). The name "Boquillas" is applied to both the American and Mexican villages, to the north, along the Rio Grande. Thus, it seems clear that a canyon on the west flank of the Sierra Maderas del Carmen is the type locality of *H. taylori* and in the vicinity of 29°N; 102°36'W.

On 28 May 1975, Riskind and T. F. Patterson collected several live specimens of *Humboldtiana taylori* in the Sierra Maderas del Carmen (Municipio de Villa Ocampo) at 28°59'N; 102°33'W, ca. 2 km NNW of Loomis

Peak on an eastern exposure at ca. 2500 m elevation. Specimens were found in semi-stabilized, moss-covered rhyolitic talus on a steep slope in a mixed conifer forest, including *Pinus strobiformis* Engelm., *Pseudotsuga menziesii* (Mirb.) Franco and *Abies coahuilensis* I. M. Johnst. It seems likely that this locality is between 5 to 10 km, generally SSE from the type locality of *H. taylori*.

Specimens collected by Riskind and Patterson have been allocated as follows: Dallas Museum of Natural History 5364; National Museum of Natural History 758552; Philadelphia Academy of Natural Sciences 343-899; and University of Texas at El Paso 4649.

MORPHOLOGY

Shells: Morphology of shells of our specimens (Figure 1) is close to that of the type series of *Humboldtiana taylori* (USNM 596939-41; holotype and 2 paratypes). Similar variability in relationship of height to diameter is shown in both series. The proportion height/diameter averages 0.88 for the 3 types with a range of 0.84-0.97 and averages 0.95 for our 8 largest specimens with a range of 0.80-1.03. The relationship of height to width of aperture is similarly variable in both lots. In both, the columellar margin is reflected over the umbilicus.

In coloration and sculpture our specimens conform to the type and paratypes. The following applies to a representative specimen: first $\frac{3}{4}$ whorl and first $\frac{1}{2}$ of second whorl bearing low wrinkles along suture, these breaking up into rows of minute granules peripherally; rows of granules continuing onto younger whorls, gradually becoming larger and ovate with long axes oriented parallel to growth wrinkles; this beaded gridwork (Figure 2) of close-set, regularly spaced granules (ca. 4 rows per mm on youngest half of body whorl) covering remainder of

shell except area immediately adjacent to umbilicus. Periostracum yellowish-brown, thin, exfoliated on older whorls and in patches elsewhere. First $2\frac{1}{4}$ whorls uniformly tan; upper 2 of 3 dark spiral bands appearing on last part of third whorl and lowermost band on fourth whorl; bands of approximately same width, slightly diffuse at edges; shell color predominantly brownish-tan (lighter than bands) with several irregular, elongate yellow blotches; margin of peristome yellowish; reflected columella light pinkish-brown.

The pattern and amount of yellow blotching is variable among specimens. Width of brown bands is also variable with the central band very narrow in one specimen. In one specimen minute granulation is present dorsally on all but the first half of the embryonic whorl.

Coloration of living animal: (Live specimens were not available to DRAKE, 1951). Largest specimens: tentacles dark brown distally, grading to brownish-orange proximally; dorsal surface (head to tail) comprised of raised areas with intervening, narrow sulci, raised areas in narrow, close-set rows on top of head, larger and reticulate in arrangement elsewhere; raised areas dull brownish-orange dorsally, grading to red-orange around margin of foot; sulci dark gray on top of head, grading to lighter gray elsewhere; outer border of sole of foot light red-orange, with remaining, central area grayed white; collar of mantle bright yellow-green.

In 3 semi-adult specimens the color of the raised areas of the dorsal and lateral region was a bright red-orange. Seemingly this color changes to dull brownish-orange with maturity except in the area around the top and sides of the foot.

Genitalia: (Figures 3, 4). A description for one specimen that was dissected is as follows: penis subcylindric, 3 times as long as broad, contracted verge long, extending 65% of length of penis, with several transverse folds, terminating in 4 finger-like processes, 2 being half as

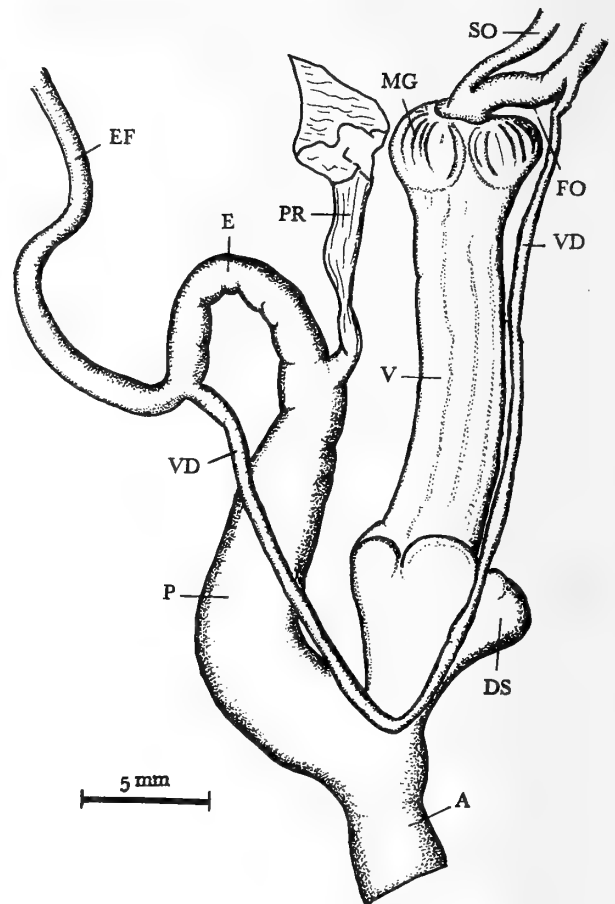


Figure 4

Lower region of the genitalia of a specimen of *Humboldtiana taylori*
 A - atrium DS - dart sac E - epiphallus
 EF - epiphallic flagellum FO - free oviduct
 MG - mucus gland P - penis PR - penial retractor muscle
 SD - spermathecal duct V - vagina VD - vas deferens

Explanation of Figures 1, 2, 3, and 5

- Figure 1: Shells of *Humboldtiana taylori* Drake, 1951, from Sierra Maderas del Carmen, Coahuila, México, showing variation in morphology $\times 1.2$
 Figure 2: Detail of shell of *Humboldtiana taylori* showing grid-work of elongate, raised granules $\times 3$
 Figure 3: Genitalia of a specimen of *Humboldtiana taylori* $\times 0.9$
 Figure 5: Fossil shell (probably of Pleistocene age) of *Humboldtiana* cf. *H. taylori* from Serranías del Burro, Coahuila, México. $\times 1.6$

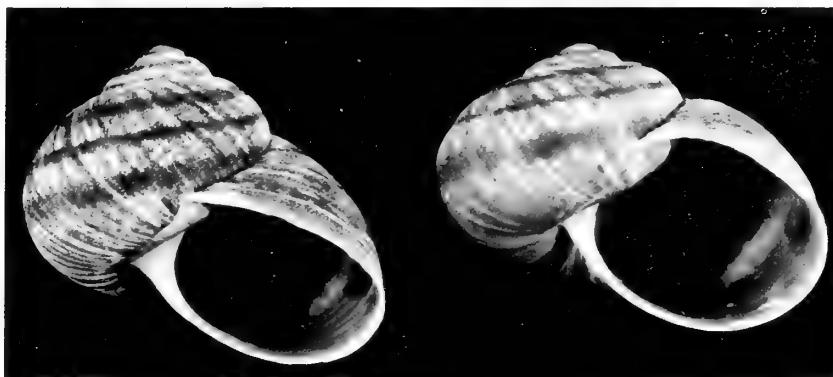


Figure 1



Figure 2



Figure 5



Figure 3

wide as the other 2; inner penial wall of lower half of penis bearing 5 wide, lengthwise-oriented ridges (irregularly further subdivided to some extent), these ridges merging at mid-length of penis and bearing nodular outgrowths that constrict penial cavity to allow only for passage of verge (no upper chamber discernible in penis); epiphallus with internal ridges; flagellum long, 3.5 times as long as combined length of penis and epiphallus; vagina long, slender, bearing 4 dart sacs, 2 smaller by $\frac{1}{4}$ than the others; mucus glands widely separated (14.2 mm) from dart sacs; spermathecal duct long, terminating in large, ovate bulb and bearing at $\frac{5}{8}$ of its length a short appendix. Measurements for the above and one additional specimens dissected are (in mm): Shell diameter, 37.2, 36.3; length of penis from penial retractor insertion to atrium, 17.0, 16.2; length of epiphallus, 14.1, 17.0; length of epiphallallic flagellum, 109.0, 86.0; length of penial retractor muscle, 9.1, 12.3; total length of vagina, 27.0, 26.5; length of free vagina (atrial junction to base of dart sacs), 4.0, 3.8; length of largest dart sac, 4.3, 4.9; length of smallest dart sac, 3.5, 2.8; distance from top of dart sacs to base of mucus glands, 14.2, 14.3; height of mucus gland ring, 3.8, 3.2; length of spermathecal duct plus terminal bulb, 93.6, 92.0; length of spermathecal appendix, 10.6, 13.0.

One radula inspected possessed 109 teeth in each of several rows counted with outermost marginals very much reduced. When handled, living specimens of *Humboldtiana taylori* produced a clearly discernible odor.

COMPARISONS

PILSBRY (1927: 168) and BURCH & THOMPSON (1957: 2) defined 2 groups in the genus *Humboldtiana*, one group having the mucus glands of the vagina situated close above the tops of the dart sacs, whereas, in the other group, dart sacs and mucus glands are separated by a distance equal to or exceeding the length of the dart sacs. BURCH & THOMPSON (*loc. cit.*) noted that members of the latter group also have a relatively longer verge and lack a conspicuous chamber in the upper penis, in contrast to the former group. PRATT (1971: 434) deemed the penial features noted to be more diagnostic than the vaginal features in separating the two groups. *Humboldtiana riskindi* Fullington & Zimmerman, 1977, also from Coahuila, is indicated by its authors (p. 136) as having some characters of both groups.

Humboldtiana taylori clearly belongs to the group of *H. texana* Pilsbry, 1927, a categorization used by PRATT (1971: 429) in reference to the second group discussed in the preceding paragraph. It has a long verge and lacks a discernible upper compartment in the penis. It is extreme in regard to anatomically known species of *Humboldtiana* in the great degree of separation between dart sacs and mucus glands and in the length of the penis (when compared with data presented by SOLEM, 1974: 363; table 1). None of the species listed by Solem show the combination, observed in specimens of *H. taylori*, of relatively short free vagina and long dart sac-mucus gland separation. Thus, on the basis of anatomical characters of the genitalia, *H. taylori* seems to be a distinctive member of the group of *H. texana*.

Fossil shells (Figure 5) of a *Humboldtiana* having the size, configuration and sculpture of *H. taylori* have been taken in the Serranías del Burro (see Introduction) in the upper end of Cañon el Bonito (29°02'40"N; 102°06'30"W).

ACKNOWLEDGMENTS

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Examination of a Reproductive Cycle of *Protothaca staminea* Using Histology, Wet Weight-Dry Weight Ratios, and Condition Indices

BY

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(4 Text figures)

INTRODUCTION

THE NORTHERN LIMIT for the littleneck clam, *Protothaca staminea* (Conrad, 1847), is Prince William Sound, Alaska (R. Baxter, Alaska Department of Fish and Game, personal communication). The clam is abundant in the Sound where it is preyed upon by sea stars, sea otters, and humans (PAUL & FEDER, 1973, 1975). Information on growth and recruitment is available for the littleneck clam in Alaskan waters (PAUL & FEDER, 1973; PAUL *et al.*, 1976; NICKERSON, 1977). In addition, the size at maturity and time of spawning for *P. staminea* has been examined in British Columbia, Canada (QUAYLE, 1943) and south central Alaska (NICKERSON, *op. cit.*). The major objective of this investigation was to determine the reliability of using dry weight-wet weight ratios and condition indices to describe a reproductive cycle of *P. staminea* in Prince William Sound, Alaska. Histological examination of gonadal tissue was used as a basis for comparison.

MATERIALS AND METHODS

Samples were typically obtained monthly in Simpson Bay (Figure 1) from January 1973 through January 1974. Dates of collection (January 1, February 20, March 6, April 7, May 7, June 6 and 14, July 1, August 12, September 28, October 26, November 30, December 30, January 20) were determined by tidal cycles and weather conditions.

Simpson Bay is located in southeastern Prince William Sound, approximately 16 km from the town of Cordova (Figure 1). Air temperatures ranged from -8° to $+13^{\circ}$ Celsius during the study period. The National Ocean Survey in 1973 recorded mean surface water temperatures in Cordova as a minimum of $+1.2^{\circ}\text{C}$ in January and a maximum of $+12.8^{\circ}\text{C}$ in July. Beach surface temperatures during the study ranged from -1.2°C in January 1973 to $+12.5^{\circ}\text{C}$ in August. During the winter, freezing of shallow tide pools and sediment surfaces was common.

Histological examination was made of 264 clams. The gonadal mass of each clam was removed and preserved in Bouin's fixative. A cube of preserved gonadal tissue was removed from the mid-lateral portion of the visceral mass, dehydrated in alcohol, cleared in xylene, embedded in paraffin, sectioned at 10–20–30 μm , and stained with Ehrlich's hematoxylin (DAVENPORT, 1960).

A gonadal staging method was used to describe the reproductive cycle (see BAYNE, 1976; PORTER, 1974; ROPES, 1968; ROPES & STICKNEY, 1965 for discussion of staging techniques). Six gonadal phases are described: early active, middle active, late active, ripe, spawning, and post spawning.

Females

Early active – Typified by the presence of follicular tissue partially or completely filling the alveoli, the proliferation of primary oocytes, and the elongation of these oocytes between follicle cells. Residual ova and cellular debris often present.

Middle active – A reduction in central follicular tissue with a subsequent increase in diameter of the central

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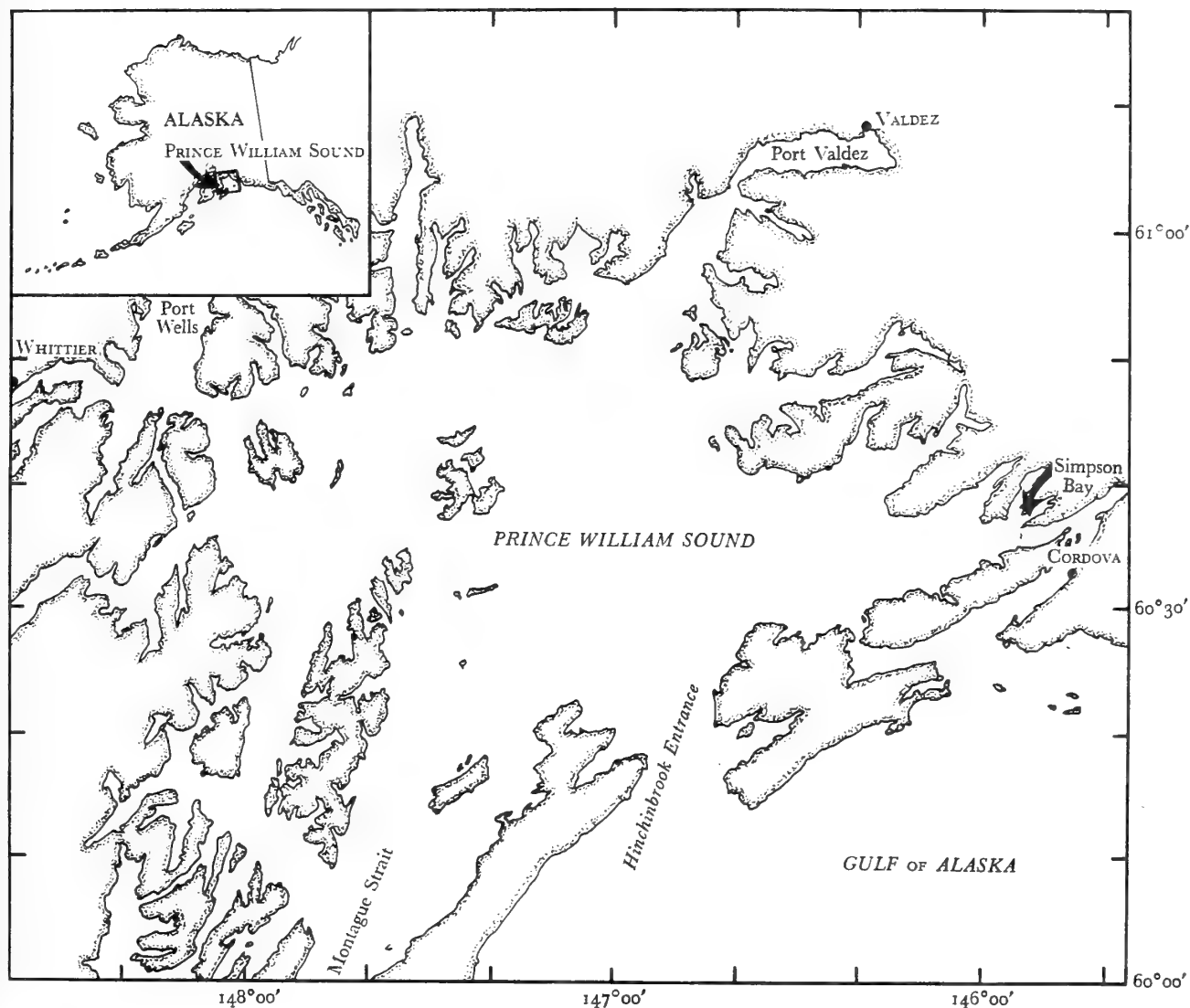


Figure 1

Map of Prince William Sound, Alaska, showing the location of Simpson Bay where specimens of *Protothaca staminea* were collected for this study

alveolar lumen. An increasing number of stalked oocytes protrude into the lumen.

Late active – Most ovocytes spherical with slender stalks; many show amphinucleoli (see ALLEN, 1953 for

importance of amphinucleoli in determining ripeness of ova).

Ripe – A majority of ova free of the alveolar wall. Ripe ova and remaining late ovocytes prominent.

Spawning – Follicle cells generally reduced to 1 or 2 rows but seldom absent. Alveoli partially emptied of ripe ova.

Post spawning – Follicle cells beginning to fill in the alveoli. Some primary oocytes appearing between follicle cells. Some free ova still present. Amoebocytes abundant within and in the vicinity of the ovary.

Males

Early active – Follicular tissue partially or completely filling the alveoli. Characterized by the presence of primary spermatocytes on the germinal epithelium, and the appearance of some spermatids.

Middle active – Follicular cells have disappeared. Spermatids arranged in radial rows.

Late active – Characterized by a central lumen within the alveolus. Spermatids have increased in number. Appearance of some spermatozoa.

Ripe – Spermatozoa fill the alveolus in thick radial columns with their tails projecting into the central lumen.

Spawning – The appearance of free spermatozoa within the alveolus. Formation of a single row of follicle cells at the alveolar membrane with more appearing as spawning proceeds.

Post spawning – Alveoli nearly filled with follicle cells with a few residual spermatozoa present. Primary spermatocytes have begun to appear on the germinal epithelium.

The meats of an additional 199 clams were dried to a constant weight, at 80°C, and dry meat-wet meat values calculated. All clams were approximately the same size.

A condition index ($\frac{\text{Dry Meat Weight}}{\text{Internal Shell Volume}} \times 100$) was calculated for 168 of these clams (see WALNE, 1970; WESTLEY, 1961, for methodology). A condition index was not calculated for January 1973. The technique of HUBBS & HUBBS (1953) is used to compare monthly values for dry-wet weight ratios and condition indices. A significant difference ($\alpha=0.05$) is demonstrated by this technique when the standard errors of the means of the 2 values to be compared fail to overlap.

RESULTS

HISTOLOGICAL STUDY

Females

The females were in an active stage for the first 4 months of 1973 (Figure 2). In May, 25% of the clams were

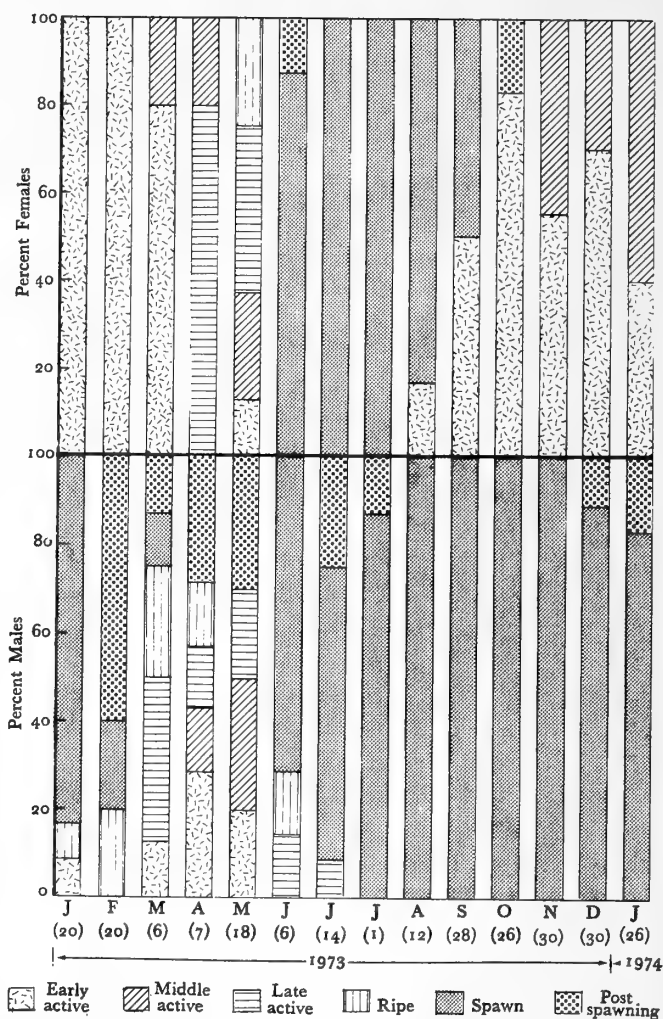


Figure 2

The female (above) and male (below) reproductive cycles of *Protothaca staminea*. The length of each shaded area represents the percent frequency of clams in each reproductive phase.

ripe; all others were in one of the 3 active stages. In June most of the individuals were in the spawning phase, some post-spawning individuals were present. All females were in the spawning stage in July. By August over 80% were still in the spawning phase; the rest were in an early active state. An increasing percentage of females in the early active stage was evident in September and October. In October some post-spawning individuals were also present. A spent phase was not observed. No spawning stages

were present in the last 4 months. Clams from November 1973 through January 1974 were in early and middle active stages.

Males

All reproductive stages were present for the first 3 months of the year (Figure 2). In April and May all stages, except spawning, were present; early active stages were found only in small males. From June through January, the majority of males were in the spawning phase. A spent condition was never observed.

WEIGHT RELATIONSHIPS

The period preceding spawning, January 20 to May 18, was characterized by a steady increase in the ratio of dry to wet meat weight (DWR; Figure 3). Initiation of

spawning was reflected by a significant ($\alpha=0.05$) decrease in DWR during the period of May 18 through June 6. The ratio continued to decline until July 1, when spawning was apparently completed. Thereafter, DWR increased significantly, and then remained relatively stable until January 1974, when an increase occurred.

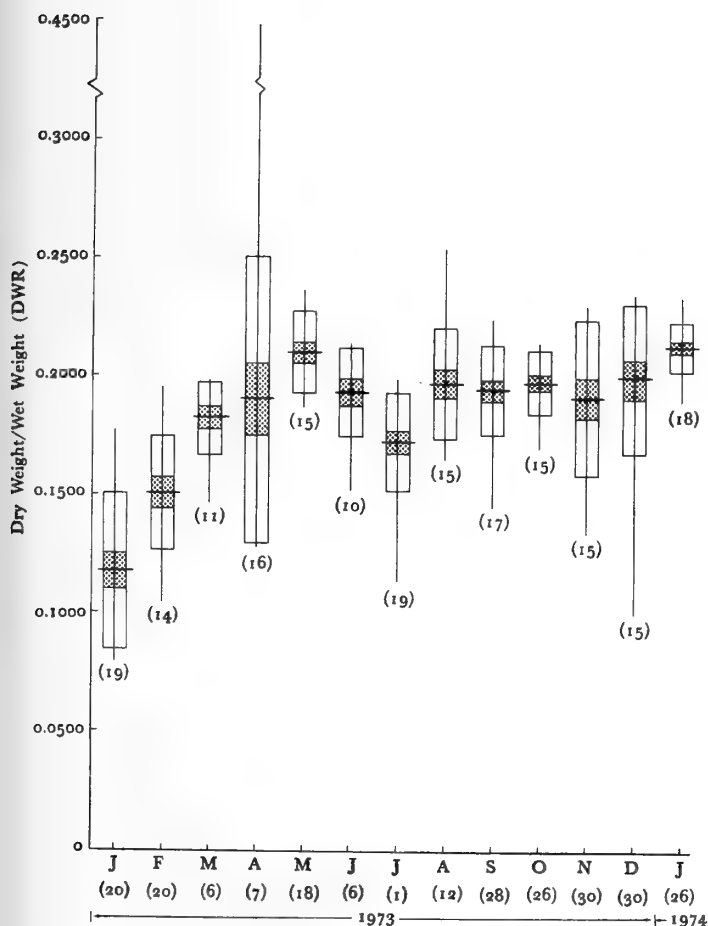
CONDITION INDEX

The condition index (CI) was lowest in February and March 1973. Significant ($\alpha=0.05$) increases in CI occurred monthly from March 6 to May 18, the months preceding spawning (Figure 4). A significant decrease in CI, representing spawning, was observed between June 6 and July 1. In general, there was little change in CI from July through December. An increase in CI occurred in January 1974.

DISCUSSION

HISTOLOGICAL STUDY

Histological examination of the female reproductive cycle indicates a single annual reproductive period for *Protothaca staminea*, with ovaries in a spawning phase from early June through September (Figure 2; NICKERSON, 1977). However, instead of entering a spent phase, where alveoli were empty of ripe ovocytes, many ripe or residual ova (or both) were present after the major spawning in June (Figures 3, 4), and follicle cell development was evident in most females during the final months of the spawning phase. Initiation of spawning by males also occurred in June (Figure 2), but a spawning period was less clearly defined. Males were in a spawning phase throughout most of the year. The maintenance of



(← adjacent column)

Figure 3

Dry meat weight/wet meat weight (DWR) indices for a spawning cycle of *Protothaca staminea*. The single vertical line represents the range, the white box the standard deviation, the dark box two standard errors of the mean, and the horizontal line the mean. A significant difference ($\alpha=0.05$) is demonstrated when the standard errors of the means of two values fail to overlap. The total number of clams examined each month is included in parentheses

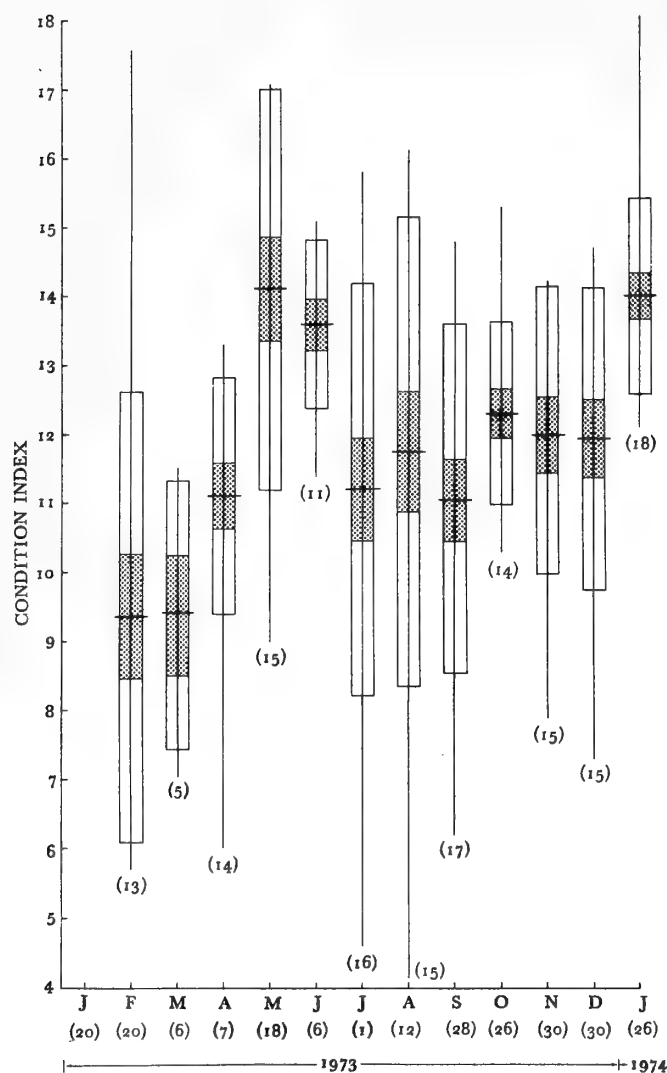


Figure 4

The condition indices for a spawning cycle of *Protothaca staminea*.

The single vertical line represents the range, the white box the standard deviation, the dark box the two standard errors of the mean, and the horizontal line the mean. No condition index was calculated for January, 1973. A significant difference ($\alpha=0.05$) is demonstrated when the standard errors of the means of two values fail to overlap. The total number of clams examined each month is included in parentheses.

a minimal level of gonad development throughout the year has been previously reported for other Veneridae (see ANSELL & TREVALLION, 1967, for discussion).

WEIGHT RELATIONSHIPS AND CONDITION INDEX

The dry weight-wet weight ratio (DWR) decreased significantly from May 18 to June 6 (Figure 3). The decrease in this ratio and the histological observation of post-spawning females in early June (Figure 2) suggest initiation of spawning occurred prior to June 6. A concurrent significant decrease in the condition index (CI) did not occur during the same period. The decrease in DWR was probably the result of water uptake after initiation of spawning. Increase in water content of bivalve tissues at the time of spawning has been documented for other bivalves (ANSELL & TREVALLION, 1967). In the calculation of CI, only dry tissue weight and shell volume are considered, and water uptake is not observable. Only a decrease in dry meat weight will be detected by the CI method. Thus, only a limited spawning took place before June 6. However, a significant decrease in CI occurred between June and July, indicating a major release of gametes at this time (Figure 4).

The high values for DWR and CI in January 1974, as contrasted with January 1973, suggest a better state of health for the clam population or a greater retention of gametes in 1974, or both. The reasons for these differences in DWR and CI at these times are unknown.

CONCLUSIONS

Calculations of weight ratios and condition indices are necessary to determine the period of peak spawning for *Protothaca staminea* in Prince William Sound. With histological techniques alone, male littleneck clams appear in a spawning condition throughout most of the year and female clams for 4 months of the year. The weight relationship studies show that the major spawning effort of *P. staminea* is restricted to the month of June.

In British Columbia, spawning occurs from April to October (QUAYLE, 1943). A shortened spawning period is characteristic of clams at the northern and southern limits of their range, and appears to be primarily a temperature-related phenomenon (see discussions by BAYNE, 1976; ORTON, 1920; WILSON & HODGKIN, 1967, on factors controlling reproductive cycles).

SUMMARY

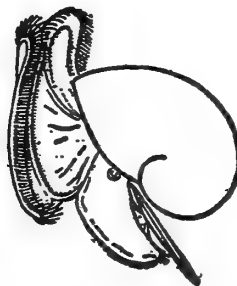
The annual reproductive cycle is described for the littleneck clam, *Protothaca staminea*, in Prince William Sound, the northern limit of its range. Reproductive activity was determined by histological examination of gonads and by calculation of monthly dry meat-wet meat weight ratios and condition indices. Histological examinations suggest that females and males are in a spawning phase from June until September and June to January, respectively. However, dry weight-wet weight ratios indicate a limited spawning in late May with continued spawning during June. Condition indices indicate intensive spawning in June.

ACKNOWLEDGMENTS

This work is a result of research sponsored by the Alaska Sea Grant Program cooperatively supported by the NOAA office of Sea Grant, U. S. Department of Commerce, under Grant No. 04-3-158-41, and by the University of Alaska with funds appropriated by the State of Alaska. We thank the crew of the R/V *Acona* and Merle Hanson for aid in collection of specimens. This work is Contribution No. 379 from the Institute of Marine Science, University of Alaska, Fairbanks.

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Life-Cycle Completion
of the Freshwater Clam *Lasmigona compressa*
(Bivalvia : Unionidae)
in an Experimental Host, *Lebistes reticulatus*

BY

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THERE ARE ONLY A FEW WORKS ON the known hosts of North American freshwater bivalves of the family Unionidae, and in most cases the host is a freshwater fish (the occurrence of *Simpsoniconcha ambigua* on the mudpuppy, *Necturus*, is an exception), although in a few cases, such as with *Strophitus undulatus*, *Anodonta imbecilis* and *Obliquaria reflexa*, there may be no fish host and development proceeds directly (FULLER, 1974).

Lists of fish hosts of the various bivalves are scattered widely in the literature, but are summarized in LEFEVRE & CURTIS (1912) and especially in FULLER (1974). Hosts of the clam investigated in this study, *Lasmigona compressa* (Lea, 1829), are not mentioned in these studies, nor does the present work deal with the normal hosts for this species. The purpose of this paper is to call attention to a system of glochidial infection and metamorphosis which is easy to study in the laboratory, since the clam is abundant in its range. The experimental fish host is the easily obtained pet guppy fish, *Lebistes reticulatus*, and the whole life cycle (*i.e.*, maturation of the larval clam) takes less than 2 weeks. Since attachment of larval hooked glochidia occurs on the fins and not on the gills, the infection can be easily observed with a dissecting microscope. The fins infested with glochidia can be easily removed for more detailed examination at any time during development by simple excision.

Adult *Lasmigona compressa* were collected from the Huron River, in Washtenaw County, Michigan, in Au-

gust, 1978. These clams were maintained in a 72 L capacity aquarium with river vegetation. The clams were given Tetramin flakes of fish food with the expectation that they would feed upon this; previous experience in this laboratory had shown that various clams do well on this diet for 6 months and longer.

Female clams of this species were found to pass glochidia – as well as orange colored ova – into the water in December, for a period of one week. Free glochidia were taken from the bottom of the aquarium with a long pipette rather than being dissected out of the gills as performed by other workers (LEFEVRE & CURTIS, 1912), for it was found that glochidia removed by dissection were noninfective. The glochidia are $320\text{ }\mu\text{m} \times 260\text{ }\mu\text{m}$ when closed, and each hook (one per valve) is $90\text{ }\mu\text{m}$ long. The hooks are studded with rather sharp little spines, $7\text{ }\mu\text{m}$ in diameter, 3 per row for much of the hook's length. About 100 glochidia were placed into each shallow Petri plate with water, and male and female guppies were allowed to swim in this for a period of 2-5 minutes, during which they were continuously examined under a dissecting microscope. This interval of time was sufficient to allow an average of 10 glochidia to attach to each fish. A heavier infection was thought to be undesirable because of the small size of these fish. Similarly, goldfish of 5 cm length were also exposed to glochidia in separate containers. Usually, 10 fish of each species were used per experiment.

The goldfish were found to attract glochidia, causing the latter to attach to the fins, but the infections were not successful; these larval clams fell off or were shed in 2 days and died.

The first infections of guppies were successful in the sense that glochidia attached well to all the fins. But after the infected guppies were isolated and kept in aerated tap-water, every one of 10 fish developed fungus infections at the sites of attachment and the glochidia died and fell off in 4-6 days. Not a single larva metamorphosed under these conditions. Uninfected fish kept in the same water remained completely healthy and free of fungus.

A separate group of guppies was then infected, but placed into aerated tap-water into which Furazone (Dyna-Pet, Campbell, Calif.) was dissolved at the concentration recommended for fish by this company to discourage bacterial and fungal growth. Under these conditions, glochidia remained attached to all the guppies, and the former underwent successful metamorphosis. The criterion for metamorphosis is only generally defined, but involves the young clam falling off or detaching itself from the fish fin after showing some adult features, especially the development of a large, muscular foot with which the young clam now crawls. Gills are also visible at this time. No significant growth was seen during this period. The time for completion of metamorphosis under these laboratory conditions, at room temperature (20°C) was 10-12 days with almost 100% success.

When the glochidia finally detached from their hosts, they were placed into aerated tap-water, containing the small freshwater diatom, *Navicula pelliculosa*. The glochidia kept in this water inside a 50 mL glass-stoppered flask lived thus and grew for 2 weeks, after which the experiments were terminated. During this time, a new growth-margin developed on each clam shell, amounting to an added new width of 46 μ m. This new growth area was characterized by a smooth surface, unlike the original glochidial shell surface, which is coarse, and studded with large calcium carbonate crystals.

A few simple experiments were conducted on the newly shed glochidia, which apparently live only one or two days unless they find a suitable fish host. Under normal, quiet conditions, the glochidia lie with the 2 valves spread widely apart, ventral side upward; these animals are normally motionless.

Several guppies were ground up in a Waring blender, and the supernatant of this fluid was added dropwise to

a dish containing quiescent glochidia. One drop of such fish fluid in 20 mL of water was enough to cause most glochidia to snap a few times, after which some stayed closed for several minutes. In 10 minutes all these glochidia were open again.

The amino acid, L-glutamic acid, was then dropped as crystals into these containers, near the glochidia. Again, a positive response was elicited, as shown by the snapping or snapping-shut of these larvae. HEARD & HENDRIX (1964) found that 20 amino acids, but not the 3 basic amino acids, arginine, histidine and lysine, elicited glochidial response in the clams which they tested.

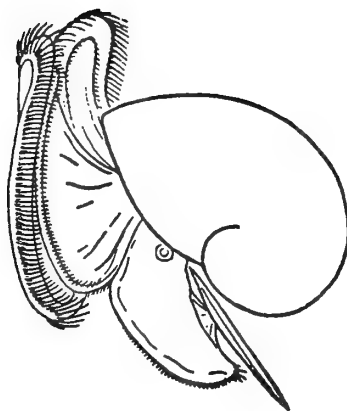
Finally, the responsiveness of glochidia to physical stimulation was tested. A very fine, etched piece of tungsten wire was used to touch various areas of the glochidium, to see if pure mechanical stimulation is enough to elicit contraction, *i.e.*, attachment behavior, and if so, to see which part of the glochidium is most sensitive. It was found that the glochidia are indeed sensitive to mechanical stimulation, without prior chemical sensitization. The most sensitive part of the glochidium was in a swelling near the hinge line, where a larval thread has been shown to originate in other glochidia (see WOOD, 1974).

It is possible that glochidia of other species could also infect the guppy under similar laboratory conditions. Such a system as this one, with *Lasmigona compressa* and the guppy, followed by feeding with *Navicula pelliculosa*, offers much promise for more detailed studies of fish susceptibility, hardness to heavy infections, for possible class demonstrations of the life cycle of freshwater clams, and especially in elucidating details of how clams metamorphose on freshwater fish. Such studies are all the more important since it is likely that this early larval life and immediate post-metamorphosis may be the most critical period in the life-cycle of freshwater clams. If such larval and young clams are more sensitive to aquatic pollution of various kinds than are adult clams, then this would explain why so many endangered areas of rivers have adult clams only and lack any (recruitment of) young. More detailed studies along these lines could be of great help in re-establishing clams into recently cleaned up rivers and ponds using some method of commercial or laboratory rearing of the young.

Voucher specimens of *Lasmigona compressa* and the infected fish have been deposited in the collections of The University of Michigan, Museum of Zoology.

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Philippia (Psilaxis) radiata:
Another Indo-West-Pacific Architectonicid
Newly Found in the Eastern Pacific (Colombia)

BY

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(1 Plate; 1 Map)

INTRODUCTION

IN 1976 I REPORTED the discovery of the architectonicid *Heliacus trochoides* (Deshayes, 1830) on the mainland coast of Ecuador (ROBERTSON, 1976b). The species had previously been known only between South Africa and the Marquesas. The present paper records a similar extension of known range for a second architectonicid, *Philippia (Psilaxis) radiata* (Röding, 1798). This species too had been known only between South Africa and the Marquesas (ROBERTSON, 1970, fig. 5). The new record of it is from a single empty shell collected in September 1977 at Gorgonilla, Gorgona Island (2°57'N; 78°12'W), about 30 km off the mainland Pacific coast of Colombia, 6500 km ENE from the Marquesas.

ACKNOWLEDGMENTS

I am grateful to the malacological group of the Universidad del Valle, Cali, Colombia (Jaime Ricardo Cantera Kintz, Francisco Borrero, Rafael Contreras, Elizabeth Buttkus and Fernando Zapata) for donating the specimen to the Academy of Natural Sciences of Philadelphia (ANSP 348879) and for allowing me to publish this paper on their discovery. The work was supported in part by National Science Foundation Grant DEB76-18835.

COLOMBIAN SHELL

(Figures 1 to 3)

Description: The fairly thick, brown and white shell is 12.2 mm high and 16.0 mm wide, with 4.9 teleoconch

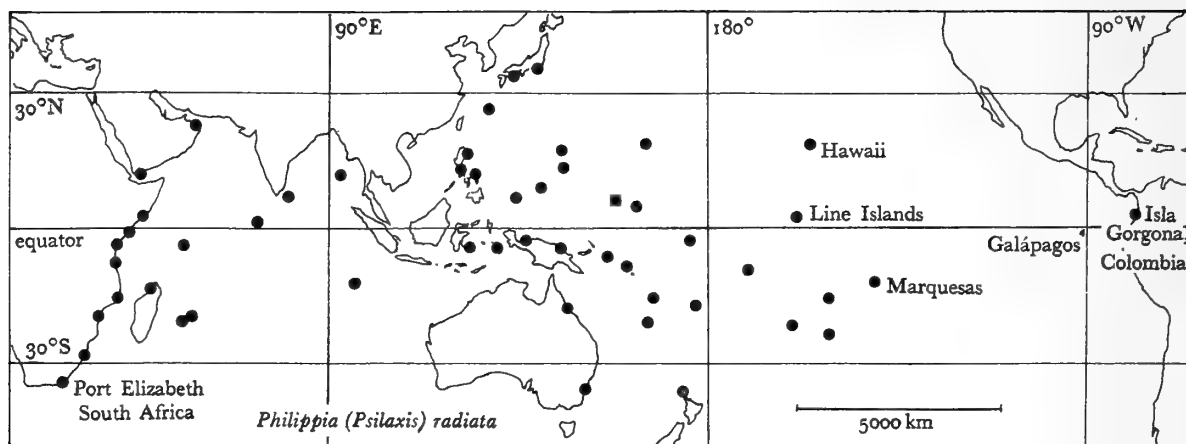
whorls. The outline is trochiform, with the spire fairly high and rounded in profile. The spire angle steadily decreases from about 130° to about 100°, but cannot be measured accurately because of the roundness. The whorls are moderately inflated. The abapertural half of the shell is much more corroded than the apertural half.

The protoconch is fairly large (1.2 to 1.3 mm in immersed width), with a short anal keel. (Both these characters distinguish *Philippia radiata* from the closely similar species *P. oxytropis* A. Adams, 1855.) The protoconch is not visible through the narrow teleoconch umbilicus.

The apical side of the teleoconch is smooth, and mainly brown with numerous radii extending to the periphery (about 28 on the last whorl) (the name *radiata* came from these radii). At the periphery there is one spiral cord bordered on either side by a fainter cord. The upper suture is attached to the lower side of the major peripheral cord.

The basal side of the teleoconch is mainly smooth. Outwardly there is a wide brown spiral band. Inwards from this are some brown spiral lines. There are two periumbilical sulci; the cord between them is checkered with about 20 brown marks. There are irregular periumbilical nodes (about 12 of them on the last whorl); these are white (or tinged with brown near the aperture). The umbilicus is narrow (1.5 mm wide). (*Philippia oxytropis* would have a wider umbilicus.) The umbilical wall is recessed, and is smooth except for axial growth lines. The umbilical suture is outside the periumbilical sulci.

The outer lip is straight in profile, prosocline, at an angle of 20° to the axis of coiling. The aperture is more or less oval in outline. There is a deep channel opposite the periumbilical nodes, a shallower channel opposite the cord between the periumbilical sulci, and a faint third



channel the other side of the deep channel. Periostracum thin, pale yellowish brown. Operculum missing.

DISCUSSION AND CONCLUSIONS

This constitutes the first record of the genus *Philippia* Gray, 1847 in the Eastern Pacific (ROBERTSON, 1976a). The species is in the subgenus *Psilaxis* Woodring, 1928 (ROBERTSON, 1970, 1973) and is definitely *Philippia (Psilaxis) radiata*, not the closely similar Pacific Ocean species *P. (P.) oxytropis* or the Atlantic Ocean species *P. (P.) krebsii* Mörch, 1875.

Protoconchs in the subgenus *Psilaxis* are noteworthy for their large size (1.2 - 1.8 mm in diameter). The veliger larvae remain for a long time in the plankton and are transported great distances by near-surface ocean currents (ROBERTSON, SCHELTEMA & ADAMS, 1970). It is likely that the Colombian animal was transported as a veliger from Polynesia - just as was hypothesized for the Ecuadorian *Heliacus trochoides* (ROBERTSON, 1976b).

There is no indication that breeding populations of either species are established in the Eastern Pacific.

Adult *Philippia* feeds on scleractinian corals (ROBERTSON, SCHELTEMA & ADAMS, 1970). The empty shell of *P.*

Figure 4

Geographic records of *Philippia (Psilaxis) radiata* (Röding) from ROBERTSON, 1970: fig. 5 and the Colombian record herein. The two literature records from the Gulf of Suez are probably erroneous and have been omitted

radiata was collected at Isla Gorgona under a stone on a muddy rock substratum. Some of the corals around the island are species of *Pocillopora*, *Porites* and *Pavona*.

EMERSON (1978) has published a useful review of the mollusks with Indo-Pacific faunal affinities in the Eastern Pacific. COSEL (1977) recorded *Mitra mitra*, another Indo-West-Pacific gastropod from Isla Gorgona.

The paucity of marine species common to the Indo-West-Pacific and the Eastern Pacific means either that there is a barrier to larval dispersal east to west and west to east or that larvae are transported the requisite distances but encounter ecological barriers which prevent the successful establishment of breeding populations. The latter explanation seems to hold for *Heliacus trochoides*, *Philippia radiata*, and other species known to have long-distance larvae. It is noteworthy that no Eastern Pacific species seems to occur sporadically in Polynesia (the currents flow prevailing in the westward direction).

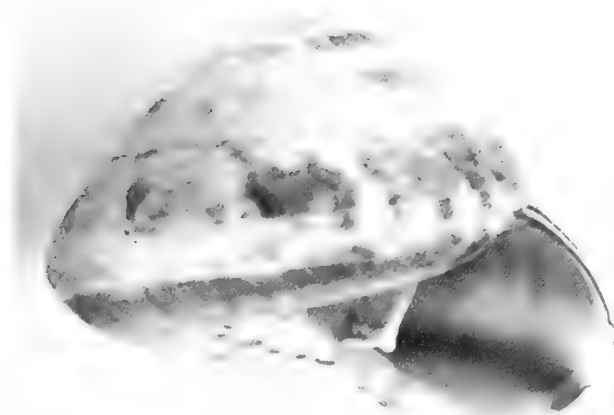


Figure 1



Figure 2

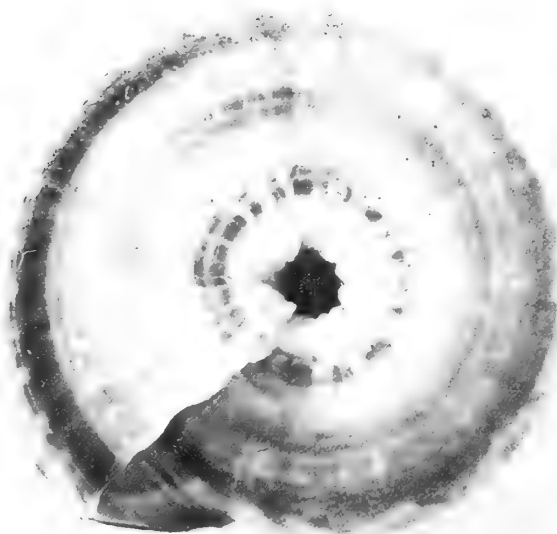


Figure 3

Philippia (Psilaxis) radiata (Röding)

Isla Gorgona, Colombia.

Shell 16.0 mm wide

Figure 1: apertural view

Figure 2: apical view

Figure 3: basal view

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The Packaging of Ova in the Egg Cases of *Aplysia californica*

BY

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(5 Text figures)

INTRODUCTION

THE MARINE MOLLUSK *Aplysia* is a prolific egg-layer. Large animals are known to lay about 5×10^8 eggs during the several months of their reproductive life (MACGINNIE, 1934). Egg-laying behavior has other interesting features. Animals generally do not lay small amounts of eggs continuously, but deposit a large number in all-or-none episodes (KUPFERMANN, 1970; KANDEL, 1976). In addition, egg-laying is one of the rare examples of a behavior in which the neurobiological substrate underlying it is relatively well understood (for reviews see KUPFERMANN, 1972; KANDEL, *op. cit.*). A hormone controlling egg-laying is released by 2 cell clusters called bag cells; each cluster contains about 400 neuroendocrine cells. The active egg-laying hormone released by the bag cells is a polypeptide with a molecular weight of approximately 6000 dalton (TOEVS & BRACKENBURY, 1969; GAINER *et al.*, 1974; ARCH, 1972). A 25 000 dalton precursor polypeptide is produced in the cell bodies and is thought to be converted to a small molecule that is transported along the processes of the bag cells for release (ARCH, 1972). In response to an appropriate stimulus, the bag cells discharge synchronously, causing the hormone to be released into the neurohemal sheath (KUPFERMANN, 1970; KUPFERMANN & KANDEL, 1970; ARCH, 1972; PINSKER & DUDEK, 1977; DUDEK & BLANKENSHIP, 1977). The hormone then appears to cause muscle fibers in the ovotestis to contract, thereby triggering the first step in the release of eggs (COGGESHALL, 1967).

Once fertilized, the ova are packaged in irregular shaped egg cases (or capsules), each containing several ova. The egg cases are strung together and deposited as an egg ribbon or cordon (Figure 1). We have analyzed certain aspects of egg-laying in wild specimens of *Aplysia californica* in the laboratory and have examined the factors that determine the varying number of eggs that are

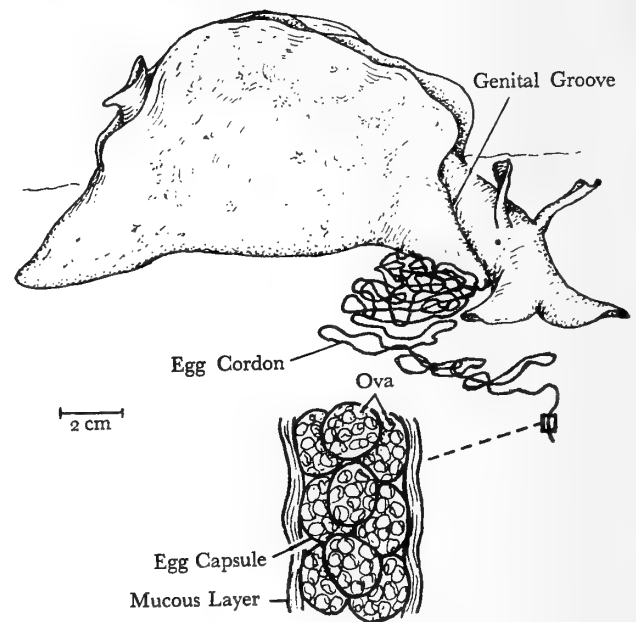


Figure 1

Egg laying in *Aplysia californica*. The adult deposits egg masses consisting of a long string of egg capsules, each containing varying amounts of eggs (after KRIEGSTEIN *et al.*, 1974)

packaged in each egg case by different animals of the species. Two aspects of this problem have often been commented upon (for review see BRIDGES, 1975; SWITZER-DUNLOP & HADFIELD, 1977). First, what accounts for the considerable observed variability in the number of eggs per capsule in the egg masses of different individuals of the same species? Thus SWITZER-DUNLOP & HADFIELD (*op. cit.*) found 5 to 7 eggs per capsule in *A. dactylomela*,

while OSTERGAARD (1950) found 7 to 15 eggs per capsule. Are these differences related to age, individual variations or nutritional state of the parent? Second, what accounts for the marked differences in the number of eggs per capsule between the various species of *Aplysia*? BRIDGES (1975) suggests that among the Aplysiidae an inverse relationship exists between the diameter of the egg and the number of eggs per capsule.

In this paper we have used size of the animal as an index of age and examined the first question. We found that the number of eggs per capsule is directly related to the size (and therefore presumably to the age) of the animal. Small and young animals invariably package fewer eggs per capsule, whereas larger and older animals package many.

METHODS

Wild animals collected off the coast of California were shipped to New York and maintained in 720 L capacity, temperature controlled, recirculating aquaria at 16 to 20° C. Animals were fed a daily portion (about 10% wet body weight) of the algae *Ulva* and *Gracilaria*. No special measures were taken to induce spawning.

Spawn was collected daily, freed of excess water, and weighed. Three lengths of cordon, a minimum of 10 cm, were then measured. The weight of each section was determined as rapidly as possible and the mean weight per centimeter calculated. The mean number of ova per capsule was determined by triplicate counts on 3 randomly chosen sections (9 observations). The section to be counted was placed on a microscope slide, depressed with a cover slip and counted with a binocular microscope at 256× magnification.

To determine the number of capsules per centimeter a minimum of 3 0.5 cm portions were cut from the cordon and centrifuged at 2 000 rpm (1000×g) for 20 minutes to compact the ova. A squash preparation was made and 0.5 cm portions counted at 160× magnification. The mean number of capsules per centimeter was calculated.

The diameters of cordon and ova were determined with the binocular microscope fitted with an ocular micrometer; a standard procedure of rounding off partial units was adopted. Three cordon portions were cut at random and kept immersed in sea water. Duplicate determinations of the diameter of each portion were made with a binocular microscope at 160× magnification. After the diameters of the cordon were taken, they were each covered with a cover slip, depressed, and the diameters of 3 ova chosen at random and from different capsules were taken at 400× magnification. The mean number of

ova per centimeter was the product of the mean number of ova per capsule and the mean number of capsules per centimeter.

Coefficients of correlation (r) and lines of best fit were obtained from a least squares regression using a PDP11 laboratory computer.

RESULTS

Collections of spawn were made from (wild) animals, ranging in size from small (presumably young), weighing as little as 19 g to large (presumably older) animals weighing to 1 300 g. In the course of examining the spawn we found that the mean number of eggs per capsule of cordon ranged from 3 to 93. Because of this remarkably wide range we explored a number of variables to determine which might affect how many eggs are packaged per capsule.

We first examined the relation of number of eggs per capsule to body weight (a crude index of the age of the animals). Three sections of egg mass were examined and the mean number of eggs per capsule determined. In the 78 animals examined a linear and fairly steep correlation was found between animal weight and number of eggs per capsule (Figure 2). This correlation was **highly sig-**

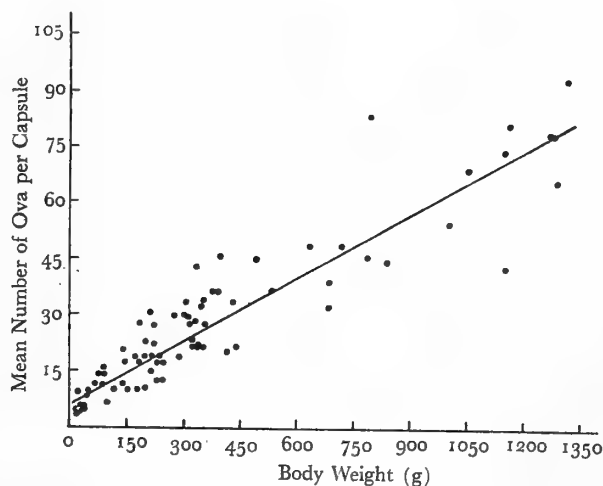


Figure 2

Mean number of ova per capsule as a function of body weight. Animals ranged in weight from 20 g to 1300 g and the ova varied in number from 3 to 93. Each datum point is the mean of 9 observations on 1 animal (see Methods for details). There is a significant correlation ($n=78$; $r=0.92$; $p < 0.01$) between the number of ova per capsule and the body weight.

nificant: $r=0.92$, $p<0.01$. Large animals packaged many more ova per capsule than did small ones. A doubling in animal weight led to roughly a two-fold increase in the number of ova per capsule.

To determine whether the increase in eggs per capsule was accompanied by large egg capsules, we next measured the number of capsules per centimeter. We found that for

animals weighing between 19g and about 450g the number of capsules per cm decreased progressively ($n=12$, $r=0.84$, $p<0.01$, $b=-0.38$). For heavier animals weighing from 450g to 1300g the number of capsules per cm decreased less ($n=43$, $r=0.77$, $p<0.01$, $b=-0.06$), even though in this range of weights the mean number of ova per capsule doubled (Figure 3A). This suggests that

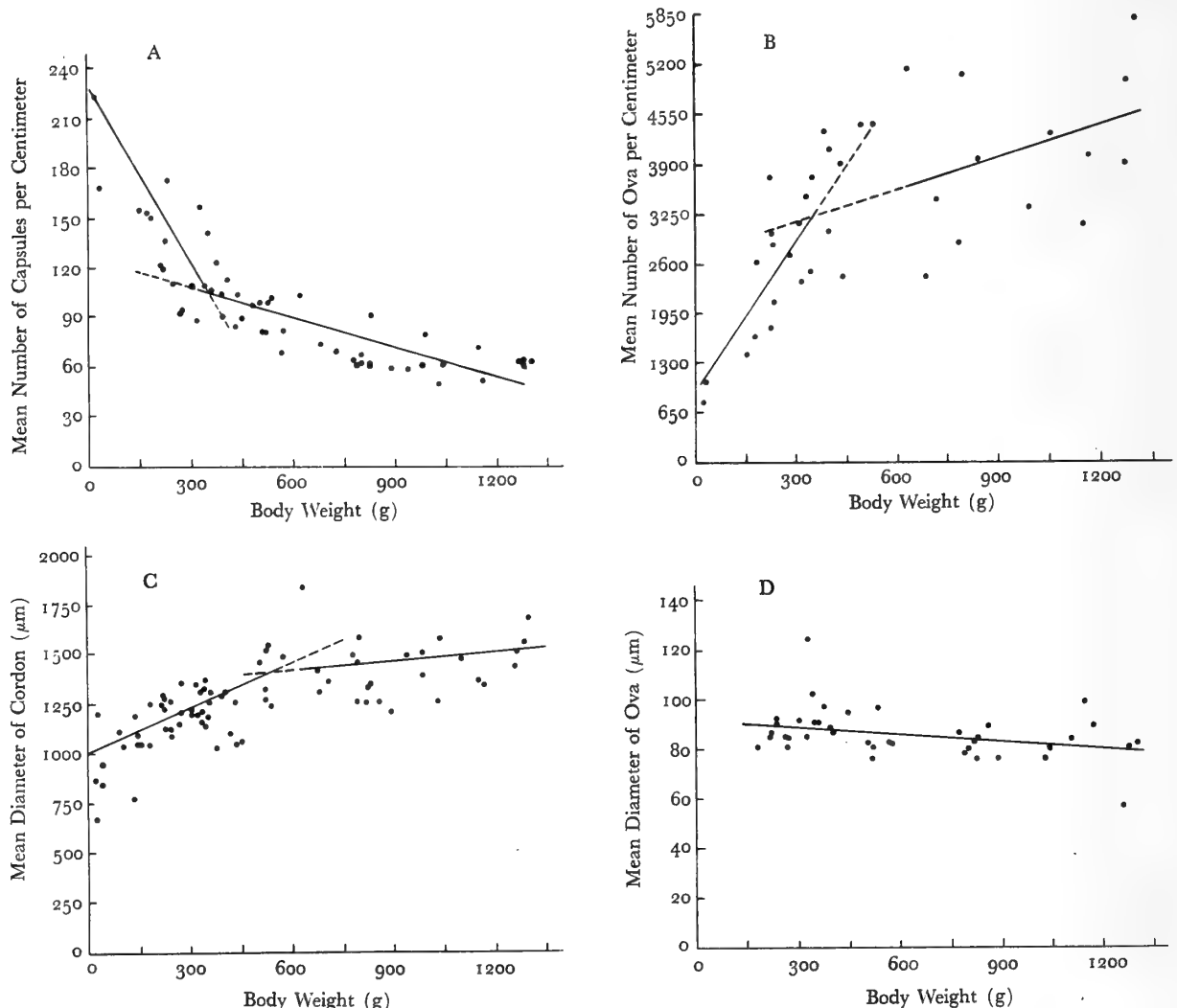


Figure 3

Quantitative aspects of egg packaging

Part A: Mean number of egg capsules per centimeter of egg string as a function of the animal's body weight. Each point is the mean of 3 observations on the same animal. The number of egg capsules per centimeter decreases markedly as the animals grow from 20g to 400g ($n=12$; $r=0.84$; $p>0.01$; slope $=-0.38$); beginning at 400g, the decrease is less ($n=43$; $r=0.77$; $p<0.01$; slope $=-0.06$). In this and in all subsequent figures, the dotted lines indicate an extrapolation of the plotted functions

Part B: Mean number of ova per centimeter of egg string as a function of body weight. The number of ova increases throughout

the reproductive life of the animal, but during later stages of the life cycle (>300 g; $n=13$; $r=0.33$; $p=NS$) the increase is less than it is early in the life cycle (20-300g; $n=22$; $r=0.79$; $p<0.01$)

Part C: Mean diameter of the egg cordon as a function of the animal's body weight. From 20g to 600g ($n=54$; $r=0.59$; $p<0.01$). From 600g to 1300g ($n=26$; $r=0.09$; $p=NS$)

Part D: Mean diameter of ova as a function of body weight ($n=40$; $r=0.38$; $p<0.05$)

up to 400 g the animal seems to compensate for the increase in number of eggs per capsule by increasing the volume of each capsule. Animals heavier than 400 g seem to pack the ova more densely into capsules of similar size. Independent measurements of the number of ova per capsule providesome of the support for this argument (Figure 3B).

As a check on this finding we explored 2 other variables: the diameter of the cordon and the diameter of the ova. We found (Figure 3C) that as animals grew up to 500 g the diameter of the cordon increased about 31% presumably indicating an increase in the size of the egg capsules ($n=54$, $r=0.59$, $p<0.1$). Beyond 600 g the diameter did not increase significantly ($n=26$, $r=0.09$, $p=ns$). This finding suggests that after a certain point the capsules remain about the same size or at least increase less. Although this finding could simply indicate that the same sized egg capsules are simply packed differently, we also found that the size of the ova decreased slightly (about 13%) as a function of size of the animal (Figure 3D).

Is there a correlation between the weight of the animal and the total number of eggs deposited? To answer this question we examined the weight of the spawn as a function of weight of the animal and found a roughly linear correlation ($n=64$, $r=0.70$, $p<0.01$) between these 2 variables (Figure 4A). Although there was a great deal of variability, small animals tended to lay small amounts of spawn (less than 1 g), large animals tended to produce great amounts of spawn (more than 25 g). When we next compared the relation of spawn as a percent of body weight to body weight (Figure 4B) we found that independent of size, animals produce egg masses that were about 2.1% of their body weight (with a range of 0.22 to 5.9%).

DISCUSSION

We have examined the egg laying capability of *Aplysia californica* as a function of age; using weight of animal as a crude index of age (see KRIEGSTEIN *et al.*, 1974; COGGESHALL, 1976). Two key findings emerge from this study: 1) animals produce spawn throughout much of their postmetamorphic life. Animals as small as 19 g (1.5% of maximum body weight in our samples) already produce viable ova; 2) the number of ova packaged per capsule varies systematically with aging.

On the basis of these findings we propose a schema illustrated in Figure 5. As animals grow they package progressively more ova per egg capsule than do smaller animals. At first the increase in ova per capsule is com-

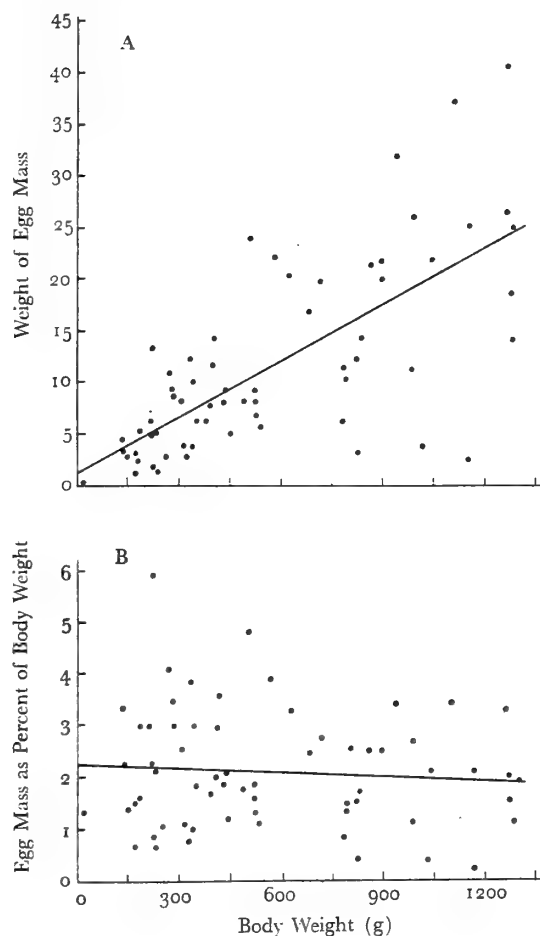


Figure 4

Egg mass and body weight

Part A: Weight of the egg mass as a function of body weight. The egg mass increases progressively from < 1 g to > 25 g as the animals mature ($n=64$; $r=0.70$; $p<0.01$)

Part B: Egg mass as percent of total body weight ($n=64$; $r=0.11$; $p=NS$)

pensated for by an increase in size of the capsule (see middle age animals in Figure 5). However, beyond 600 g the size of the capsule may not keep pace with the increase in the number of ova per capsule, resulting in a relatively tighter package of ova (old animals; Figure 5). The mechanisms that determine the density of packing and the consequences for the ovum of alterations in density are interesting questions that need now to be explored.

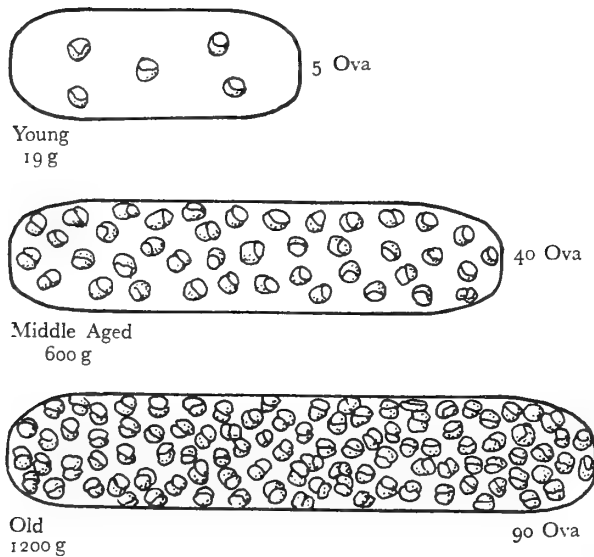


Figure 5

Schematic drawing indicating changes in number of ova per capsule and inferred changes in packing density

Larger animals also lay larger (more) spawn than do smaller animals. This increase in spawn is a reflection of the fact that animals generally lay egg masses of a relatively fixed average percentage – about 2% of their body weight.

ACKNOWLEDGMENTS

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Modiolus aurum Osorio, spec. nov.,
from Juan Fernández Archipelago, Chile

(Mollusca : Bivalvia : Mytilidae)

BY

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(9 Text figures)

INTRODUCTION

IN 1970 I RECEIVED 21 specimens of *Modiolus* from Juan Fernández Archipelago. Specific identification was not possible, because of encrusting epizoans. In 1973 another sample of 97 specimens came in, not only without epizoans, but more representative and in better condition. Some additional specimens then were noted in the collections of the National Museum of Natural History of Santiago.

ODHNER (1922) cited "*Modiola plumescens* Dunker, 1868" as occurring on Juan Fernández Island, but SOOT-RYEN (1959) suggested that until confirmed by further collecting this species should not be included in Chilean faunal lists. The specimen mentioned by Odhner as in the Stockholm Museum seems now to be missing. However, other specimens, from Australia, determined by Odhner as *M. plumescens*, were available to me on loan. Also I examined material from Île Nou and Broome, Australia, now in the Museum of Paris. The type locality of Dunker's species is Samoa, Viti-Ins, Uvea.

Because Odhner had only a single specimen from Juan Fernández on which to base his determination of "*Modiolus plumescens*," misidentification is understandable. The 2 forms have a similar outline. Table 1 shows the differences between the Australian and the Juan Fernández forms. As a result of the comparative study I conclude that there are 2 distinct species. For the Juan Fernández form, which is therefore considered to be undescribed, I propose the name *Modiolus aurum*, in reference to the golden color of the shell.

SYSTEMATIC TREATMENT

MYTILIDAE

Modiolus Lamarck, 1799 (*nom. conserv.*, ICZN, 1955)

Modiolus aurum Osorio, spec. nov.

(Figure 1)

"*Modiola plumescens* Dunker" of ODHNER, 1922: 221. SOOT-RYEN, 1959: 25. OSORIO & BAHAMONDE, 1970: 192. (Non *Modiola plumescens* DUNKER, 1868: 115; 1875: 175).

Description: Shell mytiliform, relatively high; dorsal margin curved, with a pronounced dorso-posterior angle; anterior margin narrow, rounded at the tip; posterior margin broad, evenly rounded; ventral margin straight. Beaks evident, located slightly behind the anterior end, close together, ligaments not evident. External surface of shell with evident periostracum of a golden-yellow color with greenish and brownish hues; periostracum well developed dorsally, becoming weak or wanting anteriorly; periostracal hairs of several patterns (Figure 2), type a-b occurring only near the umbones of larger specimens but over entire surface of small individuals; type c-d occurring only on the dorso-posterior end of large specimens; all hairs with a smooth axis, lacking denticulations.

A heart-shaped lunule present, anterior to the beaks.

Hinge area completely smooth within, broad (Figure 4), ligamental area elongate, slightly curved (Figure 4), originating behind beaks.

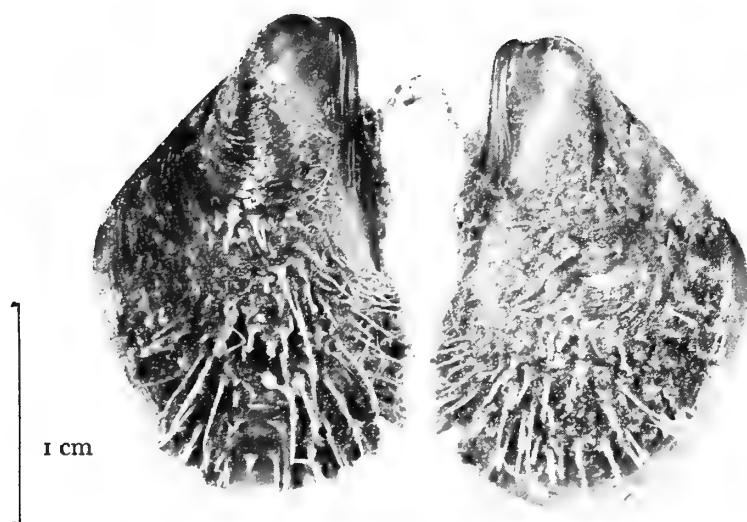


Figure 1

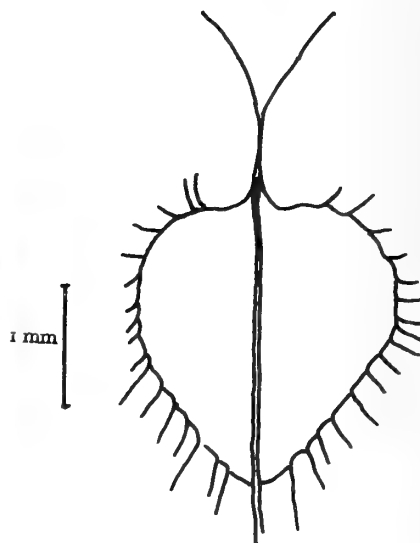
Modiolus aurum Osorio, spec. nov.

Figure 3

Lunule

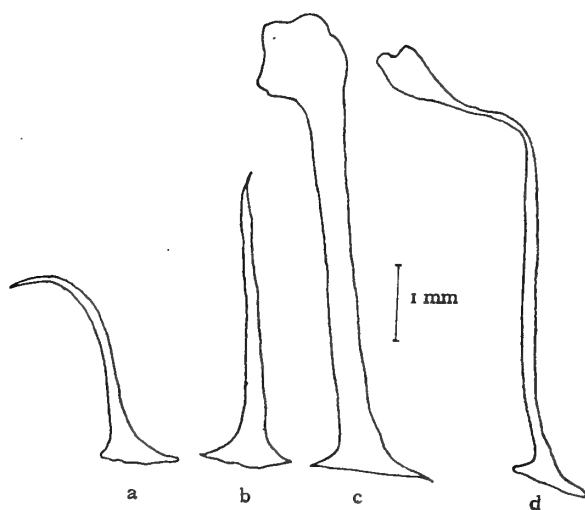


Figure 2

Different forms of "hairs" of the periostracum of *Modiolus aurum*

Muscle scars well marked, the posterior adductor sub-circular, continuous with retractor muscles, separated into 2 groups; anterior adductor small.

According to SOOT-RYEN (1955), the anatomical structures of the branchial openings have systematic val-

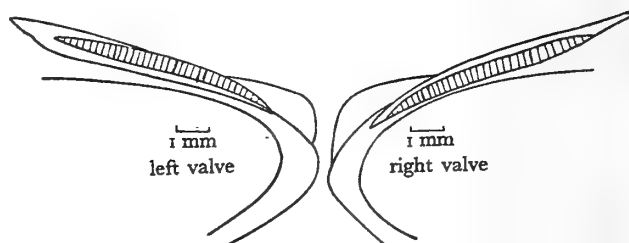


Figure 4

Interior surface of the shell, hinge area and ligament

ue; these were especially examined. The exhalant or dorsal branchial opening is oval, with thick, smooth, and well defined margins; the inhalant or ventral branchial opening is separated from it by a broad septum, the membrane prolonged laterally and slightly festooned, forming a fold that is continuous with the mantle lobules.

Type Material: Holotype, in Museo Nacional de Historia Natural, Santiago, Chile, no. 100230. Two paratypes, A 100231, B 100232. One hundred additional paratypes in the author's collection.

Dimensions: Size of holotype: length, 26.7 mm; width, 15.7 mm. Paratype A, length, 26.3 mm, width, 15.6 mm;

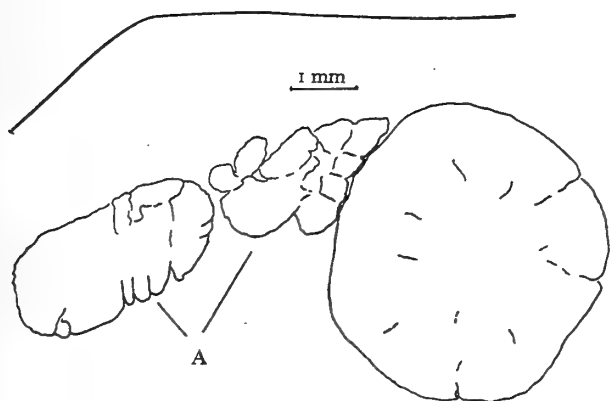


Figure 5

Muscular scars

A - retractor muscles

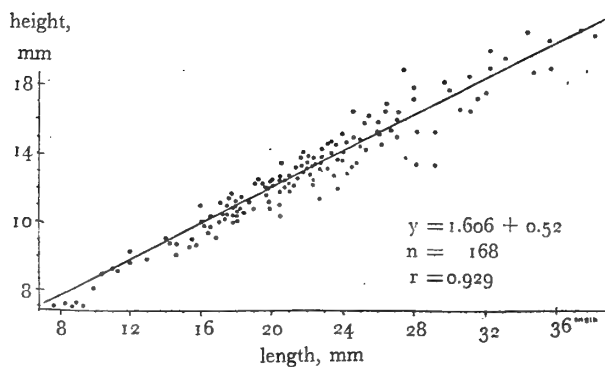


Figure 7

Proportion of length to height

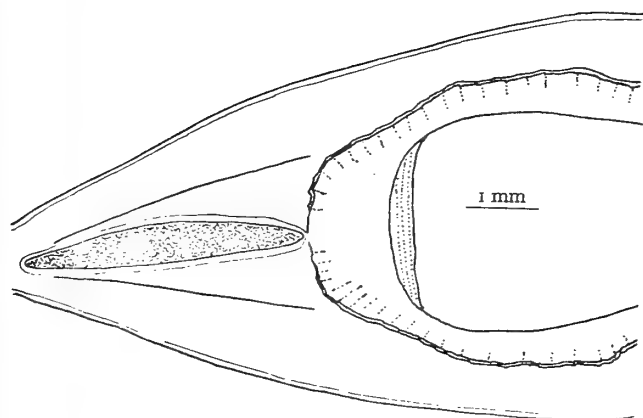


Figure 6

Branchial openings in *Modiolus aurum*

Paratype B, length, 21.8 mm, width, 13.2 mm.

Type Locality: Bahía Cumberland (Lat. 33°37'S; Long. 78°49'W).

Date: 18 April 1973.

Collectors: C. Moreno and J. Zamorano.

Substrate: on buoys or adhered to coastal rocks.

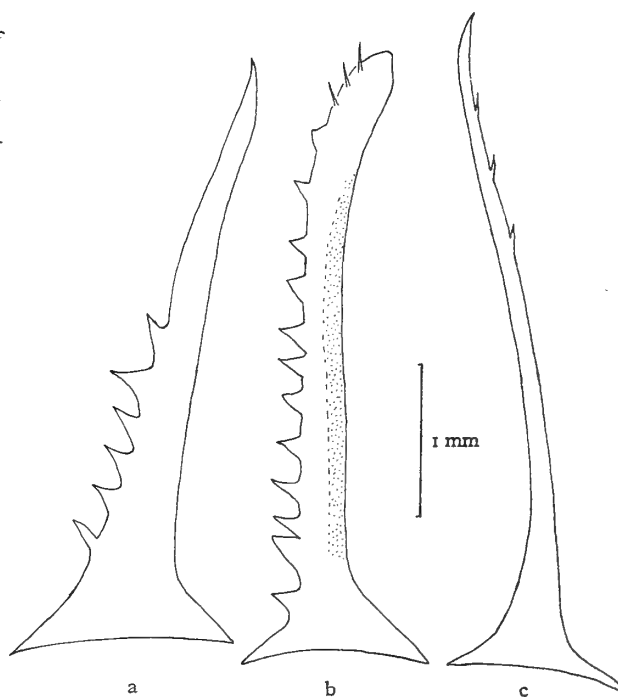


Figure 8

Different forms of "hairs" of the periostracum of
Modiolus plumescens Dunker, 1868

Table 1

Morphological differences between *Modiolus aurum* and *Modiolus plumescens*.

Characters	Species	
	<i>Modiolus aurum</i> Osorio, spec. nov.	<i>Modiolus plumescens</i> Dunker, 1868
Colour	Shells golden-yellow, with brown hues.	Shells brown-olivaceous, with reddish hues.
Lunule	Heart-shaped, small, circumscribed by a deep line (Fig. 3).	Oval, big, occupying half of the total length, circumscribed by a slight line.
Periostracum	"Hairs" of different form, axis smooth, without denticulations or membranes and its free end with diverse forms (Fig. 2).	"Hairs" of more or less similar form, axis with denticulations in a row, and its free end more or less pointed (Fig. 8).
Branchial openings	(Fig. 6). Dorsal relatively large, oval, margins smooth and well defined. Ventral clearly separated from the dorsal opening by a septum. The lateral membrane of the ventral opening terminates between the two openings.	(Fig. 9). Dorsal relatively small, oval with its inferior margin truncated. Ventral very near the dorsal opening, septum small. The lateral membrane of the ventral opening terminates by intruding into the dorsal opening.

Depth: 0 to 45 m from littoral pools to submerged objects.

Geographical Distribution:

Juan Fernández Archipelago:

- a) Robinson Crusoe Island in beaches of El Pangal, Palillo and Cumberland Bay.
- b) Alexander Selkirk Island (place of collection was not indicated).

DISCUSSION

Length-width relationships are shown in Figure 7. The linear regression was estimated, based on analysis of 168 specimens. The formula is: $y = 1.606 + 0.52x$ for the Juan Fernández population. The largest specimen measured 38.2 mm in length, 20.8 mm in width. Morphologic differences between *Modiolus aurum* and *M. plumescens* may be shown as follows.

SOOT-RYEN (1955) lists 8 species for the western coast of America, from among which KEEN (1971) indicates only 3 for South America:

Modiolus capax (Conrad, 1837) – Santa Cruz, California to Payta, Perú

Modiolus eiseni Strong & Hertlein, 1937 – Gorda Bank and Guaymas, Gulf of California to Perú

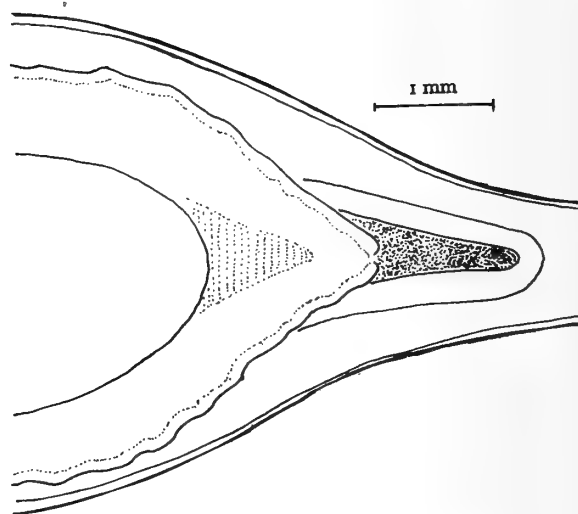


Figure 9

Branchial openings in *Modiolus plumescens* Dunker, 1868

Modiolus pseudotulipus Olsson, 1961 – Bahía Magdalena, Lower California to Perú.

All these are from tropical waters and are distinctly different from *Modiolus aurum* in form of shell, periostracal hairs, lunule, muscle scars, and branchial openings. Only *M. pseudotulipus* has a similar outline, but the unbranched periostracal hairs, broad base, and the lateral membrane distinguish it clearly from *M. aurum*.

ACKNOWLEDGMENTS

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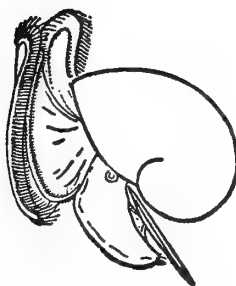
To Dr. P. Arnaud, Endoume Marine Station, Marseille, who kindly sent bibliography; to Mrs. P. Bouchet of the National Museum of Natural History, Paris and A. Andersson of the National Museum of Natural History Stockholm, for the loan of collection material.

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Range Extensions of Mollusk Species Found on the Tropical Coast of El Salvador

BY

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THE COASTS OF EL SALVADOR form part of the tropical Pacific coastline of Central America, making it part of the Panamic Province. This province extends from Cabo San Lucas (Gulf of California, approximately 30°30'N) to Cabo Blanco, north of Perú (4°15'S).

It is possible that the coasts of this region are some of the most representative of the malacological fauna in the American Pacific. STUARDO (1964) estimated the diversity of this area to be 2 200 species, including the gastropods, pelecypods, scaphopods and polyplacophorans. KEEN (1971), studying the same tropical zone, found that the diversity of mollusks is much higher and reports approximately 3 317 species.

Early in 1977, the Museo de Historia Natural de El Salvador started in a systematic manner a study aimed at an inventory of the malacological fauna of the country. To date, this work has identified close to 250 species, 26 of which are not previously reported in El Salvador (Tables 1 and 2).

Generally, the species of mollusks that inhabit the coasts of El Salvador live in environments that are relatively uniform, with gradual climatological fluctuations. STUARDO (1964) suggests that among the environmental factors having the greatest influence on these invertebrates is temperature. OLSSON (1961) reports the surface temperature of the waters of the Panamic Province as varying between 26.6° and 29.4°C, with the exception of temporary cold water upwellings.

The coasts of El Salvador are characterized by their volcanic origin; some parts demonstrate the geological history of the area (GIERLOFF-EMDEN, 1971).

The sandy beaches present a topography in which strong waves remove great masses of sand, and set up surface currents; for example, Costa del Sol, El Pimiental and Los Blancos.

Of the rocky beaches, most representative are Los Cóbano and Maculís.

Table 1

Extensions of range northward to the coast of El Salvador

Species	New northern record
Gastropoda	
<i>Tegula pellisserpentis</i> (Wood)	Los Cóbano, Sonsonate
<i>Turbo saxosus</i> (Wood)	El Tamarindo, estuary
<i>Astraea buschii</i> (Philippi)	El Tamarindo, estuary
<i>Littorina varia</i> Sowerby	Barra de Santiago and El Tamarindo
<i>Cerithidea pulchra</i> (C. B. Adams)	El Tamarindo, estuary
<i>Anachis rugosa</i> (Sowerby)	Solimar; also El Tamarindo
<i>Microcithara cithara</i> (Reeve)	Los Cóbano, Sonsonate
<i>Cancellaria bulbulus</i> Sowerby	Costa del Sol; also, El Tamarindo
<i>Conus patricius</i> (Hinds)	Costa del Sol; also, El Tamarindo
Pelecypoda	
<i>Anadara similis</i> (C. B. Adams)	Los Cóbano; also, El Tamarindo
<i>Chama buddiana</i> C. B. Adams	Maculís, La Unión
<i>Protothaca beili</i> (Olsson)	El Tamarindo, estuary
<i>Tellina ecuadoriana</i> Pilsbry & Olsson	El Tamarindo, estuary
<i>Strigilla disjuncta</i> (Carpenter)	El Tamarindo, estuary
<i>Donax dentifer</i> Hanley	Barra de Santiago; also, El Tamarindo
<i>Corbula tumaca</i> (Olsson)	El Tamarindo, estuary
<i>Periploma pentadactylus</i> Pilsbry & Olsson	Costa del Sol; La Paz

Added in Proof

Gastropoda

Cyclothyca corrugata Stearns Playa El Zonte, La Libertad

Table 2

Extensions of range southward to the coast of El Salvador

Species	New southern record
Gastropoda	
<i>Astraea olivacea</i> (Wood)	Los Cóbano; Costa del Sol; El Tamarindo
<i>Cerithium maculosum</i> (Kiener)	Los Cóbano, Sonsonate
<i>Planaxis obsoletus</i> Menke	Los Cóbano and Maculís, La Unión
<i>Acanthina tyrianthina</i> Berry	Los Cóbano, Sonsonate
<i>Solenosteira gatesi</i> Berry	Barra de Santiago and El Tamarindo
<i>Northia northiae</i> (Griffith & Pidgeon)	Costa del Sol and El Tamarindo
<i>Fusinus ambustus</i> (Gould)	Julupita, La Libertad, estuary
Pelecypoda	
<i>Cardita affinis</i> Sowerby	El Tamarindo and Maculís, La Unión
<i>Amphichaena kindermanni</i> Philippi	Metalío and El Tamarindo

Los Cóbano is characterized by having the formation of a true reef. The beach is strewn with large quantities of organic material (shell fragments mixed with sand).

In the Golfo de Fonseca (El Tamarindo, Playitas and Maculís) relatively tranquil waters provide favorable conditions for an abundant invertebrate fauna and some marine mammals.

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Added in Proof

Pelecypoda

Plicatula anomioides Keen El Pital, La Libertad

A Re-Evaluation of the Northwestern Range of the *Melongena corona* Complex

BY

ISABEL C. LEVY

(3 Text figures)

INTRODUCTION

Melongena corona Gmelin, 1791 is a common species along the coasts of Florida and eastern Alabama (CLENCH & TURNER, 1956: 171-172; pls. 100-105). This mollusk inhabits oyster bars and low energy intertidal zones. HATHAWAY (1957) completed the most thorough biological study of *M. corona*. A systematic review of the Melongenidae of the Western Atlantic was published by CLENCH & TURNER (*op. cit.*), who described the *M. corona* complex.

The *Melongena corona* complex consists of 3 morphologically different and geographically isolated subspecies: *M. c. altispira*, *M. c. corona*, and *M. c. johnstonei*. The genus as a whole is a highly variable group especially in terms of shell coloration and spination (CLENCH & TURNER, 1956: 171-172) (Figure 1).

Melongena corona altispira is distributed along the east coast of Florida, from St. Augustine to Miami. This

subspecies is characterized by a high ratio of shell length to shell width (CLENCH & TURNER, 1956: 176-178; plt. 104).

The range of *Melongena corona corona* extends from Cape Sable, Monroe County, to Keatons Beach, Taylor County, Florida; *M. c. johnstonei* is distributed from Panacea, Wakulla County, Florida to Gulf Shores, Baldwin County, Alabama. Apalachee Bay was described as an area of overlap where a clinal relationship between the 2 subspecies occurs (CLENCH & TURNER, 1956: 172). (Figure 1)

Spination is the primary morphological character used to differentiate between *Melongena corona corona* and *M. c. johnstonei* (Figure 2). The former subspecies has 2 rows of spines on the shell, a shoulder row and a basal row. The latter has only a shoulder row of spines. Coloration was used as a secondary character for subspeci-

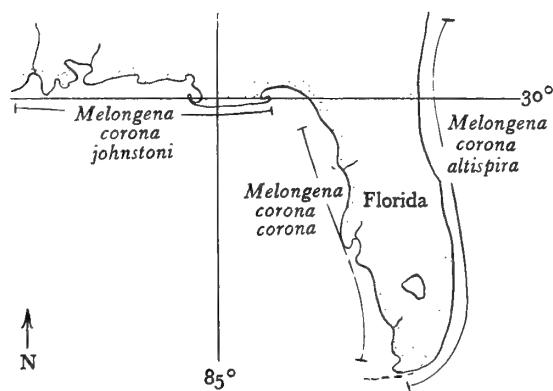


Figure 1

Map of occurrence of subspecies of the *Melongena corona* complex, according to CLENCH & TURNER, 1956

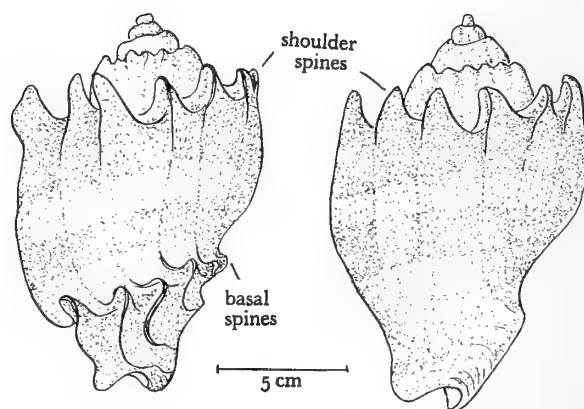


Figure 2

Subspecies of *Melongena corona* of the Gulf of Mexico
a - *Melongena corona corona* b - *Melongena corona johnstonei*

fic classification (CLENCH & TURNER, 1956: 173-174, 178; pls. 94-97, 100-103, 105).

In my preliminary studies shell spination and coloration were shown to be variable characters throughout the range of the 2 subspecies. The objective of this study was to determine the actual value of spination and coloration as taxonomic characters for the 2 subspecies: *Melongena corona corona* and *M. c. johnstonei*.

METHODS

Melongena corona were collected at 5 stations along the west coast of Florida: Pensacola (Escambia County), Port St. Joe (Gulf County), Shell Point (Wakulla County), and Seahorse Key (Levy County) (Figure 3). Samples from Pensacola and Wakulla Beach were from *Thalassia* and *Spartina* habitats, respectively. Sandflats were sampled at Port St. Joe and Shell Point; at Seahorse Key collections were made on oyster bars.

Sampling was done by collecting all *Melongena corona* found in randomly selected areas at each station. All collections were done during low tide when the majority of snails were active (not buried in the sand). Sex, shell length, shell width, shoulder width, shell color, spire length, and spination were recorded for each snail.

Spination data consisted of the presence or absence of the basal row of spines and number and size of spines. Table 1 shows the location of the stations sampled, sample size, as well as the percentage at each station of individuals with basal spines.

Sex of the snail was determined by secondary sexual characters. A prominent yellow area around the entrance to the pedal gland distinguishes mature females. The penis of males is located on the right side of the head. Immature females lack both characters mentioned.

Non-parametric tests for equality of proportions were carried out on the binomial data obtained. Relationships between the treatments (geographical location, snail size) and the effect (spination) were thus investigated. Coloration could not be quantified due to the extreme variability.

Post-hoc tests were completed on all significant chi-square values. This type of test involved pairwise comparisons between all treatment levels. In this manner the levels that caused significant frequency differences were identified.

RESULTS AND DISCUSSION

Table 2 summarizes the criteria used by CLENCH & TURNER (1956) for the subspecific classification of *Melongena corona corona* and *M. c. johnstonei*. The stations sampled in this study included the range of both subspecies and the cline between them. The cline theory by CLENCH & TURNER (*op. cit.*) was not supported by my data.

Shell color (banding) was found to be extremely variable at all locations sampled. The variability found among populations was similar to the variability represented

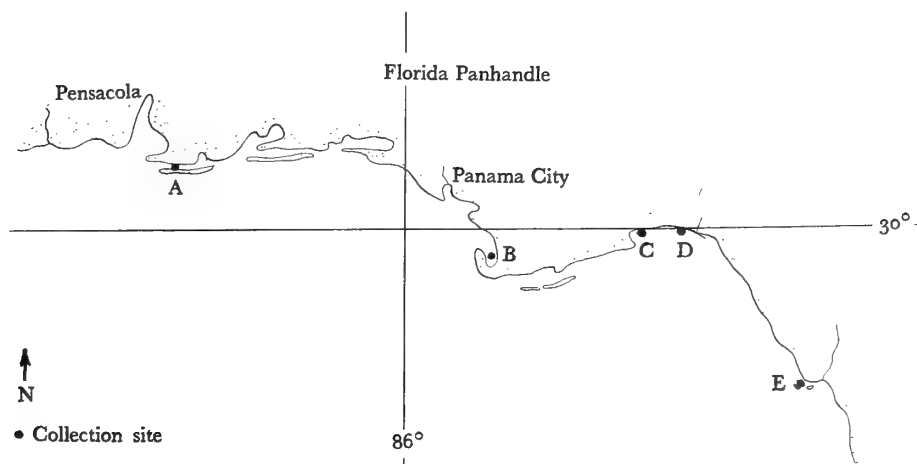


Figure 3
Florida Panhandle. Collection sites of this study

within each station. Consequently, coloration was considered an unreliable character for this species.

No difference was found in the proportion of shell shoulder width to spire length among stations sampled. Shell spination, although variable, was quantified at all locations studied. The basal row of spines (characteristic of *Melongena corona corona*) was found throughout the ranges of both subspecies and their cline (Table 1).

Table 1

Station	Location	Sample size	% with basal spines
A	Pensacola Escambia County	53	26%
B	Port St. Joe Gulf County	74	10%
C	Shell Point Wakulla County	52	79%
D	Wakulla Beach Wakulla County	61	40%
E	Seahorse Key Levy County	51	55%

The chi-square values of non-parametric tests for equality of proportions for spination as related to snail size were significant (0.01 level). In other words, the percentage of snails with basal spines is different according to size.

Post-hoc tests of these data demonstrated that snails longer than 6.1 cm exhibit higher frequencies of basal spination than snails below 6.0 cm.

Similar tests were run on shell spination with respect to geographic location. The analysis of these data showed that basal spine frequencies are different due to geographic location, the chi-square value was significant to the 0.01 level (Table 2). No trends were apparent.

The sample from Pensacola, Florida, was analyzed for sex-linked spined morphology. No statistically significant differences were found between the sexes (26.9% of males and 23.8% of females had basal spines).

The results draw attention to the fact that individuals with basal spines are not confined to the range of *Melongena corona corona*, as defined by CLENCH & TURNER (1956), but are also found throughout the range of *M. c. johnstonei*. Spination is not sex-linked, but is related to snail size and geographic location. Field data obtained on mating pairs included all possible combinations between spined and non-spined individuals.

Characters previously used for subspecific classification, other than spination, display high degrees of intrasubspecific variability and lack of intersubspecific character exclusion. Therefore, they can not be used to define the subspecies.

CONCLUSIONS

Because of their sedentary habit, encapsulated development, and absence of planktotrophic larvae, *Melongena*

Table 2

<i>Melongena corona corona</i>	<i>Melongena corona johnstonei</i>	Stations A-E
1. Shoulder is usually horizontal and narrow	1. Whorls shouldered	1. Within a given population both types were found
2. Shell reaching 205 mm	2. Shell reaching 171 mm	2. Continually growing species
3. Color. Ivory with spiral orange-brown bands, very variable	3. Color. Ivory with two or three bands of dark brown	3. Within a given population all color morphs for both subspecies were found
4. Spire subdepressed to extended	4. Spire extended	4. The spire was subdepressed to extended
5. Usually there is a single row of rather large spines at the base of the whorl. In other colonies the spines may be reduced to a single row at the shoulder whorl, the basal row being absent	5. Sculpture consisting usually of a single row of strong, erect or recurved spines on the margin of the shoulder whorl. Rarely there exists a rather weak series of spines near the base of the shell	5. All areas studied showed significant percentages of individuals with basal spines
6. May have two smaller rows of spines between the ones mentioned above	6. Not mentioned	6. Not found in areas studied

corona populations have a tendency to remain within the same area. Egg capsules that can be moved by mechanical means or tides are the most probable mechanisms of dispersal. Prior to construction of the intercoastal waterway, the only potential barrier to tidal dispersal in northwest Florida was the area between West Bay and Destin, where for approximately 80 km there are high energy beaches and no interconnecting marshes. Low energy beaches are encountered again in the Destin area, Okaloosa County, and continue along Santa Rosa Sound to Gulf Shores, Baldwin County, Alabama.

Melongena corona thrives in all appropriate habitats throughout Florida and Alabama. Due to the snail's inherent variability, small semi-isolated populations may be slightly different from each other. The *Melongena corona* complex possibly represents a polymorphic species, as opposed to a polytypic one.

Selection for certain physiological adaptations, which may or may not be apparent, are possibly due to specific environmental conditions. If the adaptations are phenotypically apparent, such morphs, as well as their delimitations are then as difficult to describe as the delimitations of their causative factors (MAYR, 1969).

Melongena corona populations from southern Florida may display a third row of spines, between the shoulder and basal rows. This character was not found in this study. The southern range of the species should be re-evaluated.

Data from the present study indicate that CLENCH & TURNER's (1956) descriptions of subspecies of *Melongena*

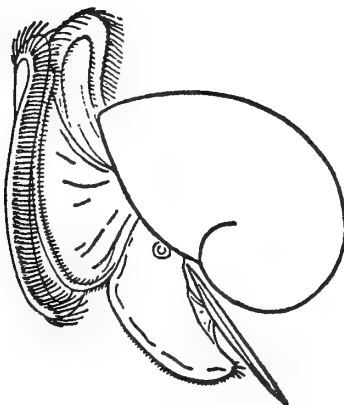
corona from the northeastern Gulf of Mexico are not valid. My data show that subspecific classification is not warranted by the characters previously used.

ACKNOWLEDGMENTS

I express my appreciation to Mr. Dan O'Leary, Jr., of Crawfordville, Florida, for allowing me to study his *Melongena corona* collection. Many thanks to Ms. Karen Swift and Ms. Sandra Mossburg for their help in the collection of specimens. I am also grateful to Dr. Jerry Oglesby for his advice on statistical procedures and Mr. Ray Johnson for his aid in the analysis of the data. This research was partially supported by an Environmental Protection Agency grant to Dr. Paul V. Hamilton. I am most grateful to Dr. Charles N. D'Asaro for encouraging me to write this paper and for the long hours he spent editing it.

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Rediscovery of the Holotype of *Cymatium (Cymatium) ranzanii* (Bianconi, 1850)

(Gastropoda: Prosobranchia)

BY

BRUNO SABELLI¹, MARCO TAVIANI^{*} AND STEFANO TOMMASINI¹

(1 Plate)

DURING A RECENT REARRANGEMENT of the malacological collections in the Zoological Museum of the University of Bologna, Italy, we found the mollusks collected by G. Fornasini from Mozambique. This material was studied by the Bolognese naturalist Giovanni Giuseppe Bianconi (1809-1878), who published on it during the period 1847-1869 in "*Specimina Zoologica Mosambicana*." He described some new species among which was a rare gastropod, a *Cymatium*. This was described as a new species by Bianconi February 21, 1850 during a meeting of the Accademia delle Scienze dell'Istituto e della Società di Bologna (BIANCONI, 1850) in the following diagnosis:

"*Triton Ranzanii*, Bianc.

"= *T. Testa fusiformi subtrigona transversim obscure sulcata, et striata, flavo rufescente, anfractibus superne angulatis, ultimo subtriangulari, ad angulum tuberculo instructum; latere sinistro bituberculato, dextro incavato; fauce postice aperta; columella nigro maculata, cauda recta longiuscula*." The following year he published the 4th part of *Specimina Zoologica Mosambicana* (BIANCONI, 1851), figuring the specimen and adding to the original diagnosis this description:

"*Descriptio. Conchylium fusiforme, oblongum, subtrigonom. In spira ejus octo circumvolutiones ad mediam cari-*

natas, declives, superne striatae, subtus vix concavae numerantur. Tubercula depressa inaequalia, et inaequaliter disposita super spiram, quaemadmodum super volutam exteriorem. Haec voluta, spiram excedens, retro valde carinata est; carina vero rotundata, quae in triangulum transversim evolvitur. Tria tubercula, unum in unoquoque trianguli angulo, duo in latere sinistro. Latus dexterum caret tuberculis, immo profunde concavum est. Superficies ultimae volutae tuberculis caret; tantummodo striis ornatur et sulculis, inter costulas sitis ut in Trit. femorale, at vix elevatis. Faux triangularis, oblonga, in latere dextero sulcata, postice valde angulata. Ejus margo dexter aliquantulum dilatatus, et undulatus; canalis omnino rectus; columella recta inferne, incavata postice, et inflexa. Color in profunda fauce violaceus: maculae brunneonigrescentes marginem inspergunt; quae majores in columella, quam usquam alibi. Facies externa, si amoveas epidermidem sive indumentum marinum filamentosum, flavo-veola est, infulis brunneis distincta."

Although the original figures of Bianconi are very fine, we think it useful to give a photograph of the holotype. In fact by comparing the 2 figures (Figures 1, 2), some differences are evident. The siphonal canal is longer and more curved than in Bianconi's figure; the aperture is apparently narrower and the upper part of the outer lip

Explanation of Figures 1 to 5

Figure 1: *Cymatium ranzanii*, holotype, Museum of Zoology of the University of Bologna × 1

Figure 2: Original drawing of *Cymatium ranzanii* from BIANCONI (1851) × 1

Figure 3: Original label accompanying the holotype, slightly enlarged

Figure 4: *Cymatium ranzanii*, holotype, apical view, Museum of Zoology of the University of Bologna × 1

Figure 5: Original drawing of the apical view of *Cymatium ranzanii* from BIANCONI (1851) × 1

¹ Istituto e Museo di Zoologia dell'Università di Bologna

^{*} Laboratorio di Geologia Marina del C.N.R. di Bologna



Figure 1

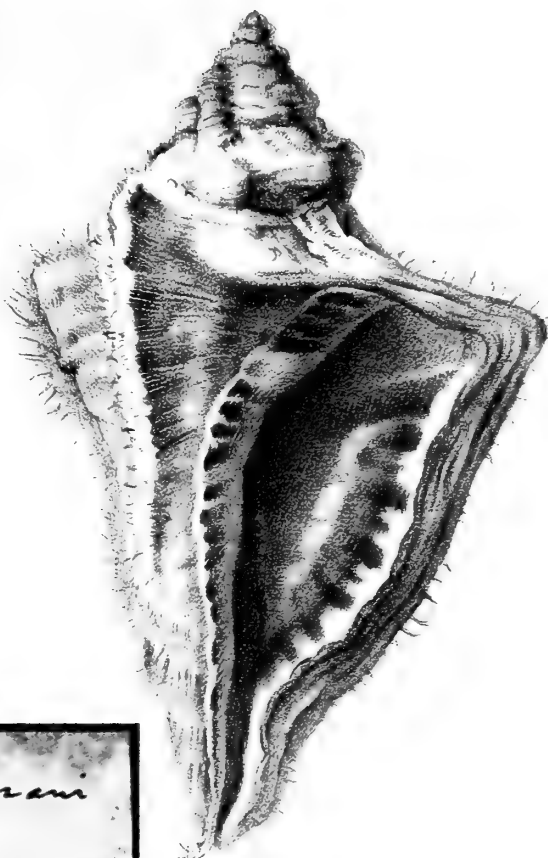


Figure 2

Triton Ranzani
No. 6.
Ex Mozambique in
Africa etc.
D. Pomarini 46

Figure 3



Figure 4

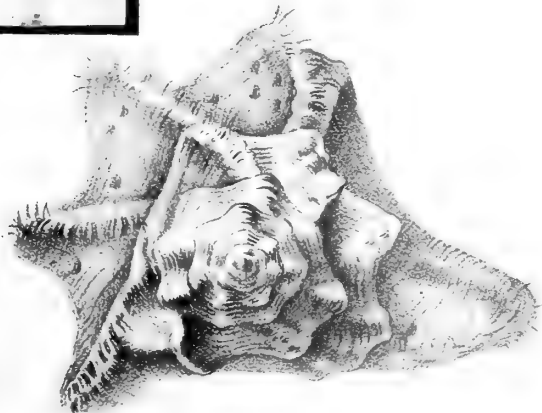


Figure 5

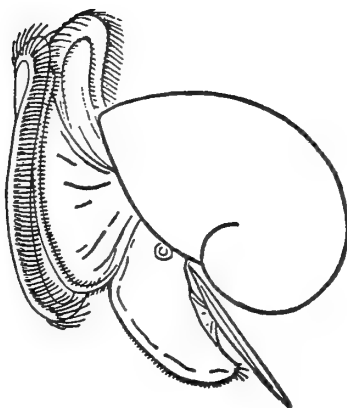
is less angular. Furthermore, the specimen was drawn slightly bent, the anterior varix thus appearing upward directed. Bianconi's figure looks to be more compact than the specimen.

The so well developed periostracum is now almost completely lost. The height of the holotype is 137 mm.

Cymatium (Cymatium) ranzanii is one of the rarest Cymatiidae, with a geographic range from the eastern part of the Indian Ocean to the East African coast and the Red Sea (MIENIS, 1976). Recently it was well figured by some authors (EMERSON & D'ATTILIO, 1962; ANONYMOUS, 1971; DANCE, 1972; KILIAS, 1973; ANONYMOUS, 1974; MIENIS, *op. cit.*). Very close but different species, according to the authors, are *C. (C.) tigrinum* (Broderip, 1833) of the Panamic province, and the Caribbean *C. (C.) femorale* (Linnaeus, 1758).

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BOOKS, PERIODICALS, PAMPHLETS

**The Family Cerithiidae in the Indo-Pacific. Part I:
The Genera *Rhinoclavis*, *Pseudovertagus*
and *Clavocerithium***

by RICHARD S. HOUBRICK. Monographs of Marine Mollusca, No. 1: 1 - 130; 98 pls. \$17.50 (15 December 1978)

Detailed taxonomic monographs seldom make good bedtime reading and are generally consulted only for making identifications or in subsequent revisionary taxonomy.

Richard S. Houbrick's recent monograph of the cerithiid genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium* contains much more than the average taxonomic monograph, and I recommend it both as a model of the diversity of information that can and should be incorporated in taxonomy and as a readable and interesting source of information and insight into a major group of tropical reef-associated gastropods that cannot be assessed taxonomically or placed in an evolutionary context working from populations of highly polymorphic shells alone. Treatment includes 47 living and fossil species.

Those involved in taxonomic research and in making phylogenetic inferences will appreciate the care with which the author has considered characters and their weighting and his explicit discussion of the data base for his concept of species. In particular, it is good to see life history and ecological data incorporated in taxonomic decision making. In addition to shell characters, morphological analysis includes soft anatomy and radular characters. Scanning electron micrographs of radulae provide a helpful adjunct to verbal descriptions, although they have contrast problems that obscure detail and fail to resolve important features. On the basis of this work we may justifiably look forward to the promised monographic treatments of additional cerithiid genera.

The format of the new journal, Monographs of Marine Mollusca, will be immediately familiar to those who know Indo-Pacific Mollusca. It is published by American Malacologists, Inc., Greenville, Delaware, under the editorship of R. Tucker Abbott and serves as a continuation of Indo-Pacific Mollusca, currently an inactive pub-

lication series of the Delaware Museum of Natural History.

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**A New Monoplacophoran Limpet
from the Continental Shelf off Southern California**

by JAMES H. McLEAN. Contributions in Science, Natural History Museum of Los Angeles County, No. 307; pp. 1 - 19; 25 figures in text. 16 March 1979

Although discovery of living coelocanths in the 1950s made larger headlines, the collecting of a living monoplacophoran - *Neopilina* - was a more signal event for paleontologists and malacologists. The deep-water habitat of that and several subsequent finds left questions about mode of life unanswered. Now a new find may bring some answers, for specimens of another new neopilinid have been taken in relatively shallow water in an area at present easy of access.

The new form is surprisingly small - less than 3 mm in length - yet, with the aid of modern techniques of study and photography, McLean and the colleagues who assisted him have been able to make detailed examination of internal and external anatomy and to obtain good radular mounts. The holotype, which is 1.94 mm in length, is figured at a magnification of $\times 100$ on a full-page plate. The photograph shows not only shell structure but also the form of the soft parts - the mouth, the foot, the 6 pairs of gills, and the mantle margin.

A new subgenus is proposed for the reception of the new species - *Neopilina (Laevipilina) hyalina* McLean, spec. nov. The type locality is on Santa Rosa-Cortes Ridge, depth 373-384 m. Other records of the species from the general region range as low as 174 m depth. A photograph of the bottom at the type locality shows small rocks thinly covered with sediment, and an early sample was on a rock fragment that was snagged up by a fishing line. We may hope that more material will now become available.

A. Myra Keen

"Evolutionary Systematics of Bivalve Mollusca":

A discussion organized for the Royal Society and the Malacological Society of London by Sir Maurice Yonge, F. R. S., and T. E. Thompson. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* (ISSN 0080-4622), Vol. 284 (1991): pp. 199-436, (paper). £17.00, overseas, postpaid. 16 Nov. 1978

This impressive issue of "Phil. Trans." is the product of a symposium held in London in May, 1977, devoted to the evolution and systematics of bivalve molluscs. Noting that $\frac{2}{3}$ of the contributors were paleontologists, and the rest distinguished neontologists and malacologists, your reviewer entered upon his task with determination, but also with some trepidation. The terminological jungle in which I found myself was at first formidable but, by dint of persistence, I came to perceive some fascinating areas new to me. I must confess I found difficult the papers by Scarlato & Starobogatov, and by Pojeta, on the early evolution of bivalves. The former authors outlined 14 orders and 25 suborders of bivalves; the latter, despite 15 crowded plates of fossil specimens, left me figuratively not seeing the forest for the trees (my own deficiency, I think, rather than that of the paper).

Stanley, in a lucid paper on the Trigoniidae, invokes both biology and paleontology to argue that the living genus *Neotrigonia* is not a "living fossil," even though it contains the survivors of a flourishing Mesozoic group, but a genus well-adapted to modern conditions. Incidentally, it is regrettable that this volume contains no paper comparable to Stanley's illuminating account of the great Mesozoic radiation of bivalves (*Journ. Paleontol.* 42: 214-229, 1968), a paper the general reader might do well to read before tackling some of the more specialized papers of this volume.

Bivalves are exceptionally favorable material for the study of evolutionary rates, by virtue of the abundance of fossil material in numerous lineages, found in extensive stratigraphic sequences for, or from which, ecological and radiometric data are available. Kauffman, in a closely-reasoned paper based on studies of many Cretaceous lineages, argues that both modes and rates of evolution (in new taxa per unit time or duration of taxa) can vary widely even within lineages. Rapid rates of species formation may occur at times of colonization of unoccupied ecological space, or during crises of eco-

logical stress. Although the "simple" bivalves have commonly been considered to have evolved slowly and steadily, the actual rates are as high as those claimed for late Cenozoic mammals! Yet one may wonder if the small differences which seem to separate fossil bivalve species may not magnify the apparent rate of speciation or, as a later contributor, Boss, puts it, whether the tendencies "to proliferate nomina and to elevate taxa partially obfuscate reality." One should read the original and judge for oneself.

To me, one of the most illuminating papers was that of Runnegar, on the pseudo-bivalved Rostroconchia, recognized as a new class as recently as 1972. Here is the group transitional between the univalved Monoplacophora and the bivalves: Paleozoic forms with a bilobed but unhinged shell, precisely fitting the "hypothetical filter-feeding monoplacophoroid with undivided shell" postulated by Stasek as ancestral to the true Bivalvia, the first of which, *Fordilla*, appeared in the Cambrian.

Waller's paper on the classification of the Pteriomorpha includes some difficult material on hinge ligaments; in this connection it is regrettable that the contribution of C. M. Yonge on the ligament of the Bivalvia is represented only in abstract. One may need to read Yonge's paper, published elsewhere (*Proc. Roy. Soc. London, B*, 202: 231-248, 1978), before Waller's.

Contributions on bivalve soft parts are fewer. Owen clarifies Atkin's groupings of Macrociliobranchia and Microciliobranchia by establishing through scanning electron microscopy that the Ostreaeidae belong to the former group, despite features other than gill ciliation that seem to contradict this placement. Allen's paper on deep-sea Protobranchia reveals that this order is of more importance in the deep sea than most of us shallow-water biologists have been assuming, and he also shows how little their shells may reveal of variation in their internal soft anatomy. Levinton and Lassen discuss enzyme polymorphism in *Mytilus* and make a case for selection of population isolates in spatially close but ecologically distinct areas, as in estuarine conditions in Long Island Sound. Boss cautions against the danger inherent in the "superfluity" of bivalve nomenclature and argues for a simplified but phylogenetically meaningful classification. The volume closes with a thoughtful analysis by Purchon of an attempt to base a bivalve classification on 9 "useful" categories of morphological data, on both soft parts and shell characteristics. This seems a wholesome trend away from

the over-reliance of paleontologists on dentition. One can return to Newell's introductory paper, "A paleontologist's view of bivalve phylogeny," with a little more understanding and a great deal more sympathy for the problems faced by those who would unravel the evolution of bivalves.

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The Genus *Arcinella* (Mollusca: Bivalvia) in Venezuela and Some Associated Faunas

by J. GIBSON-SMITH and W. GIBSON-SMITH, GEOS, Escuela de Geología y Minas, Universidad Central de Venezuela, No. 24; pp. 11 - 32; 3 pls. January 1979

This paper describes and illustrates Caribbean forms of the chamid genus *Arcinella*, from Miocene to Holocene, and plots their biostratigraphic distribution and phylogeny. Two new early Miocene species are described and a new subgenus (*Nicolia*, type-species *Chama draconis* Dall, 1903, from the Chipola Formation of Florida) is proposed. The authors' extensive collections of Venezuelan Tertiary mollusks form the basis for many additional faunal notes, bearing on the development of Neotropical faunas and Neogene chronostratigraphy of the Caribbean area. A number of synonymies in other molluscan groups are introduced, and earlier authors' accounts reappraised. The new gastropod species *Purpura weisbordi* is described from the Mare Formation of middle or late Pliocene.

Barry Roth



THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

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Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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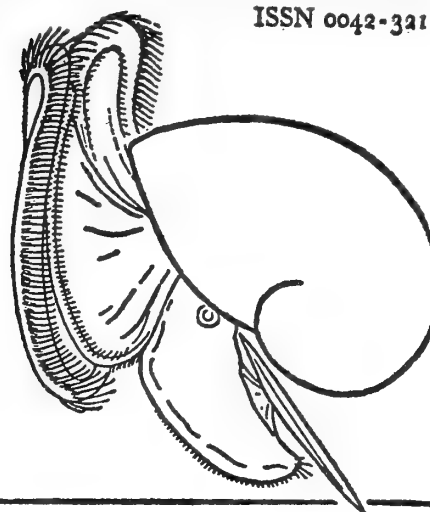
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, **DIVISION**, Subdivision, **SECTION**,
SUPERFAMILY, **FAMILY**, Subfamily, *Genus*, (*Subgenus*)
New Taxa

Acochlidium bayerfeldmanni spec. nov.,

(Gastropoda : Opisthobranchia : Acochliidae)

from Palau Islands

BY

ERHARD WAWRA

3. Zoologische Abteilung, Naturhistorisches Museum Wien, A-1010 Vienna, Austria

(2 Plates)

INTRODUCTION

AFTER I HAD SUBMITTED a manuscript on material of *Acochlidium* collected by Sutter in 1949 on the island of Sumba (BÜHLER & SUTTER, 1951), some specimens from the locality of *Acochlidium amboinense* (Strubell, 1892) in the Palau Islands, as described by BAYER & FEHLMANN (1960), were obtained.

The specimens from Sumba identified by VAN BENTHEM JUTTING (1955) as *Acochlidium weberi* (Bergh, 1896) proved to represent a new species, *A. sutteri* WAWRA (in press). Because of several discrepancies between the description of BERGH (1896) of the radula and penial armature and the results of my dissections, the Sumba specimens could not be identified as *A. weberi*. The specimens from Sumba differ also from the description of *A. amboinense* in which the penis opens to the right behind the buccal mass (BÜCKING, 1933). In *A. sutteri* a duct is formed by the penial sheath leading from the penis to the base of the right rhinophore where it opens to the outside (WAWRA, in press).

Regrettably, BAYER & FEHLMANN (1960) did not indicate where the opening for the penis in their specimens might be, whether in agreement with the description of BÜCKING (1933), whose work was based on the original specimens of STRUBELL (1892), or otherwise. Because the type material of *A. amboinense* is destroyed (Rudo von Cosel, Universität Gießen, FRG, personal communication), attempts were made to examine specimens of *A. amboinense* from Palau.

Acochlidium bayerfeldmanni Wawra, spec. nov.1960. *Acochlidium amboinense*, F. M. BAYER & H. A. FEHLMANN, Proc. Biol. Soc. Wash. 73: 185

Diagnosis: Length of living animal 25 mm, preserved 11 mm; foot well developed, 2 pairs of tentacles.

Radula: Radular formula: $1 \cdot 1 \cdot 2 \times n$, n approximately 56; left marginal plate lacking, rhachidian tooth finely serrated.

Hermaphroditic, the vas deferens leading from visceral sac to base of right rhinophore, then to penial glands; penial armature consisting of a double row of hooks and a cluster of slender thorns; penis opening at the base of right rhinophore.

Type Locality: Arakitauch River, Island Babelthup, Palau Islands (BAYER & FEHLMANN, 1969: 185)

Type Specimens: The holotype has been deposited in the Molluskensammlung, Naturhistorisches Museum, Wien, Austria (Inv. Nr. 81.232), along with 2 paratypes (Inv. Nr. 81.233: partially dissected, radula mounted in polyvinylactophenol on 2 slides with subnumbers 161, 162, and a sample of the gonad sectioned at 5 μ m and stained in Heidenhain - Azan on a third slide with the subnumber 163; Inv. Nr. 81.234: partially dissected, a sample of the gonad with the subnumber 164). One paratype has been deposited in the Naturhistorisches Museum, Basel, Switzerland (Nr. 11.117a).

The specimens were collected around the end of January and beginning of February 1978 by G. Bright.

Named in honour of F. M. Bayer and H. A. Fehlmann who were the first to work on *Acochlidium* from the Palau Islands. Unfortunately, the specimens studied by Bayer & Fehlmann have been misplaced (J. Rosewater, U. S. National Museum, Washington, D. C., personal communication).

DESCRIPTION

Preliminary Remarks: Although I have not seen the material described by Bayer & Fehlmann, I assume that it is identical, on the specific level, with the specimens received for this paper. Bayer & Fehlmann gave a detailed description of their specimens, and now only a correction and an addition to their results are necessary, the latter, however, with systematic consequences.

General Appearance: The general appearance of these Palauan freshwater opisthobranchs is similar to that of *Acochlidium amboinense* and *A. sutteri*. The only difference is that the visceral sac is smooth as pointed out by BAYER & FEHLMANN (1960: 185). This difference may not necessarily be of diagnostic value, rather it could be the result of more careful fixation in the 2 recent samples.

Radula: The radula of several species of the Acochlidacea has proved to be asymmetrical, e. g., *Hedylopsis suecica* Odhner, 1937 (MARCUS, 1953); *H. spiculifera* (Kowalevsky, 1901) (POIZAT, 1978); *H. cf. H. spiculifera* (Wawra, unpublished record); *Microhedyle cryptophthalma* Westheide & Wawra (WESTHEIDE & WAWRA, 1974); *Strubellia paradoxa* (STRUBELL, 1892) and *Acochlidium sutteri* (WAWRA, in press). Therefore, the observations of BÜCKING (1933) and BAYER & FEHLMANN (1960) needed reconsidering.

In the specimens examined, the radular formula is asymmetrical ($1 \cdot 1 \cdot 2 \times n$, $n=53$, with a few of the younger rows lost during preparation) because the left marginal plate is lacking (Figures 4 and 5). The form

and size of the radular plates otherwise correspond with the drawings and measurements of BAYER & FEHLMANN (1960) and the number of crossrows, very unlikely constant, is approximately the same. Table 1 compares the measurements of the radular elements found by BAYER & FEHLMANN (1960) and those of my own observations. Attention should be paid to the difference in size of the 2 lateral plates, although the sum of the widths on the right side plus the space between the plates equals the width of the left plate.

Table 1

Measurements of radular elements (in mm), those taken from BAYER & FEHLMANN (1960) in parentheses.

Height of rhachidian tooth	0.21-0.23	(0.24-0.27)
Width of right lateral	0.12	(0.12)
Width of right marginal	0.02	(0.03)
Width of left lateral	0.15	(-)
Height of right marginal	0.04	(0.055)

Male Genital System: The dissection of the specimens did not at first reveal any differences from the animals of *Acochlidium sutteri* until the penial sheath was opened. As in *A. sutteri*, the vas deferens, which is embedded in the right lateral body wall of the anterior body, runs parallel to the foot from the visceral sac to the base of the right rhinophore. With close inspection, this part of the vas deferens is visible from the outside as a thin cord (Figure 1). After a U-turn to the left, the vas deferens leaves the body wall and continues as a small duct running underneath another, larger duct formed by the penial sheath across the cerebral commissure to the penial glands (Figure 2).

The only difference from the animals of *Acochlidium sutteri* appears in the construction of the armature of

Explanation of Figures 1 to 3

Acochlidium bayerfehlmanni Wawra, spec. nov.

- Figure 1: Holotype, (NHMW 81.232): Female genital opening (go), vas deferens (vd) $\times 20$
 Figure 2: Paratype (NHMW 81.233): Penial duct formed by the penial sheath (pd), vas deferens (vd)
 Figure 3: Paratype (NHMW 81.233) after dissection of the penial sheath: Penis armature $\times 50$

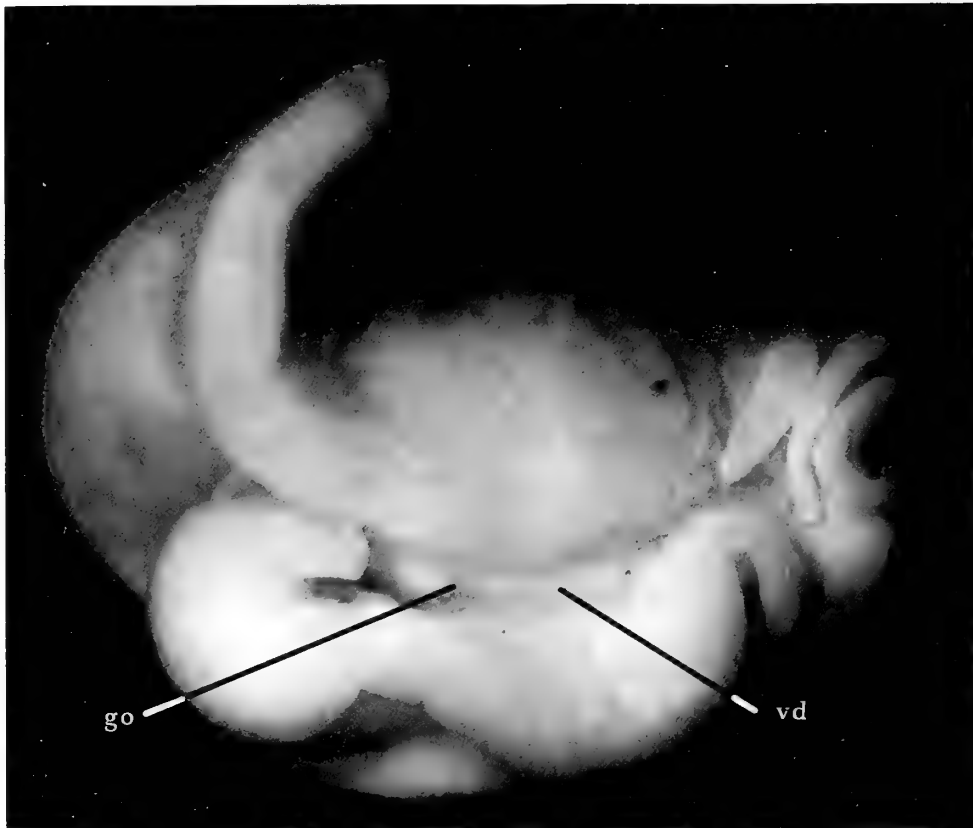


Figure 1

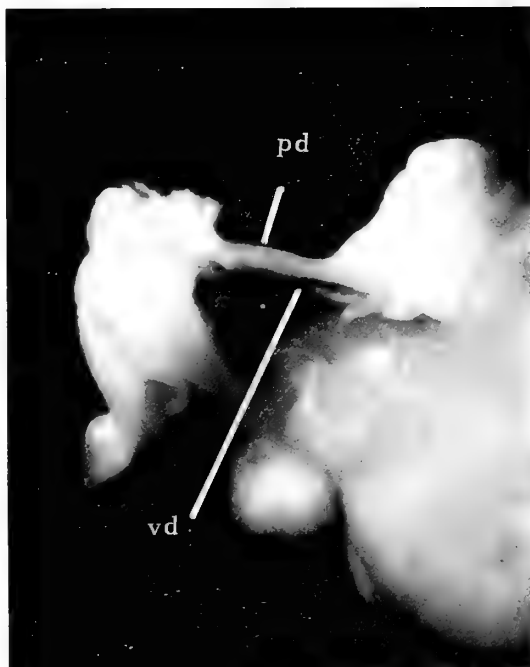


Figure 2



Figure 3

the glans penis. Whereas the penial armature in *A. amboinense*, with one longer and one shorter tip or thorn in addition to a double corona of hooks as drawn by BÜCKING (1933: figs. 6 & 7), corresponds to the armature in *A. sutteri* (WAWRA, in press, fig. 4), in the animals of *A. bayerfehlmanni* the glans penis lacks the large thorn-like ending of the vas deferens and the smaller thorn is replaced with a bundle of thin, slender thorns (Figure 3). These observations are in good agreement with the findings of BAYER & FEHLMANN (1960) with the exception that there is no free space between the smaller hooks and the thin thorns as illustrated by BAYER & FEHLMANN (1960: fig. 2b). The histological sections of a sample of the gonad taken from a specimen with a penis show a true hermaphroditic condition, spermatids and mature sperm occurring at the same time as oocytes with yolk-material (Figures 6, 7). The gonad of a specimen lacking the penis and its glands was still undifferentiated.

DISCUSSION

BAYER & FEHLMANN (1960) considered their specimens of *Acochlidium* as representing *A. amboinense* despite differences between the drawings of BÜCKING (1933) and their own observations, differences which they thought were due to different "artistic representation" or "deficiencies in observations." Insofar as the radula is concerned I would possibly agree, because my observations differ from those of Bayer & Fehlmann as well as those of Bücking. But by employing phase contrast microscopy and using a suitable mounting medium the asymmetry of the radula of *A. bayerfehlmanni* can easily be demonstrated. However, figure 4 of BÜCKING (1933) leaves the possibility for a symmetrical radula (2:1:2) in *A. amboinense*, unless there is proof to the contrary.

I cannot agree with BAYER & FEHLMANN (1960) regarding the penial armature. The same armature as illustrated by BÜCKING (1933) for *Acochlidium amboinense* has been found in *A. sutteri* and therefore it is hard to believe that BÜCKING's (1933) drawings were not precisely done. However, the description of the glans penis and its armature by BAYER & FEHLMANN (1960) is confirmed.

The slight differences in the placement of the hooks between the figures of these authors and my specimens may perhaps be caused by different muscle contraction during fixation.

One might consider the lack of the longer thorns in *Acochlidium bayerfehlmanni* as an earlier developmental stage of specimens of *A. sutteri*, but the specimens reported by BAYER & FEHLMANN (1960) were collected in September 1957 and October 1958, while my specimens were collected in January/February 1978, and none of the Palauan specimens examined had a penial armature as described for *A. sutteri*.

CONCLUSION

The gross anatomy of *Acochlidium bayerfehlmanni* indicates a close relationship to *A. sutteri* which is morphologically separated only by a different penial armature. The isolated localities of the freshwater streams of Palau and of Sumba, respectively, speak rather more for speciation than against. Differences from *A. amboinense* are more distinctive and include the location of the male genital opening, the course of the vas deferens, the penial armature, and differences in the radula, assuming a symmetric radula for *A. amboinense*.

ACKNOWLEDGMENTS

I am very grateful to Dr. E. Alison Kay, University of Hawaii, Honolulu, to her student J. Heslinga, and to Dr. Greg Bright, who together made it possible for me to obtain 4 specimens from Palau. I am also indebted to Dr. Rainer Hacker, Naturhistorisches Museum Wien, and again to Dr. Kay for critical reading of the manuscript.

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Explanation of Figures 4 to 7

Acochlidium bayerfehlmanni Wawra, spec. nov.

Figure 4: Paratype (NHMW 81.233/162): Radula, right marginal plate and distal part of right lateral plate. Phasecontrast

× 900

Figure 5: Same as Figure 4, but left lateral plate

Figure 6: Paratype (NHMW 81.233/163): Ovotestis, yolk material (yo) × 155

Figure 7: Same as Figure 6: Sperm and spermatids × 800



Figure 4



Figure 5

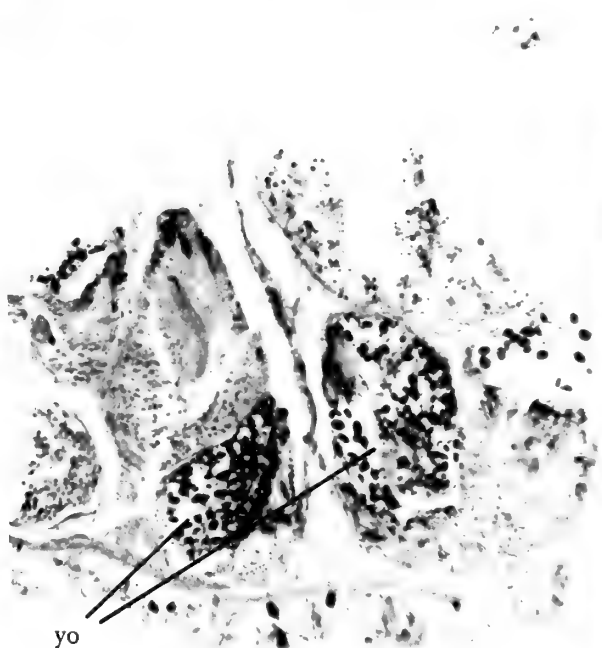


Figure 6

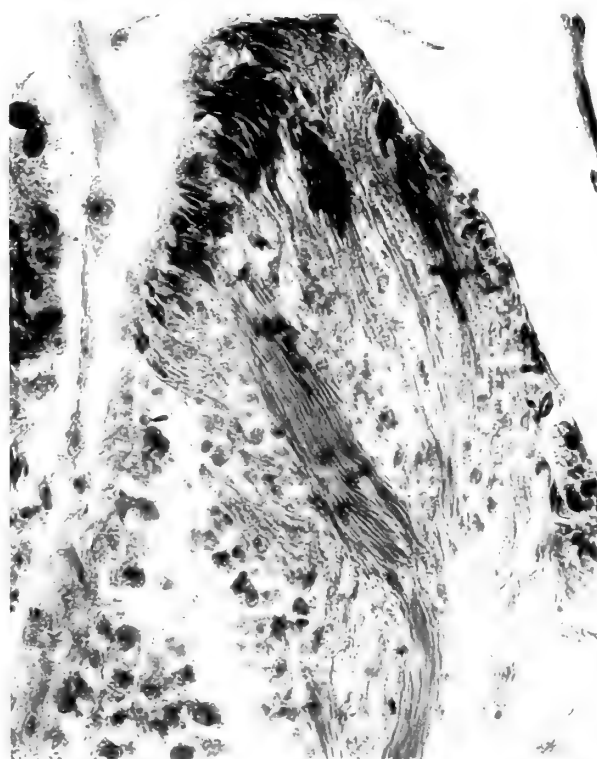


Figure 7

Variations in the Shell-Flesh Relationships of *Mytilus*: The Value of Sea Mussels as Items of Prey

BY

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(1 Text figure)

OVER THE PAST DECADE or so there has been a growing interest in the different strategies adopted by predators in their search for food. An optimal foraging strategy represents the combination of those factors associated with maximising an organism's energy intake relative to the time and effort involved in acquiring food (*e.g.*, EMLÉN, 1968; SCHOENER, 1971; CHARNOV, 1976; PYKE, PULLIAM & CHARNOV, 1977). A predator expends energy searching for and handling suitable items of prey and this must therefore be set against the amount of energy eventually yielded by the prey item. Predators feeding mainly on relatively sedentary species such as bivalves will generally select their prey on the basis of its size and availability (*e.g.*, ELNER & HUGHES, 1978; O'CONNOR & BROWN, 1977). *Mytilus*, however, which constitutes a major food resource for several contrasted predators (*e.g.*, sea-stars,

gastropods, crabs, birds) possesses a strong protective shell the size and strength of which will be a major factor in determining a predator's handling time. For practical reasons it is assumed that shell strength is proportional to shell weight (at least for mussels of similar size and shape) and the latter is known to vary not only from one locality to another but also with respect to tidal level (Table 1). Furthermore, the size and strength of the adductor muscle is also known to vary significantly even amongst mussels of comparable shell length (HANCOCK, 1965). This short communication considers the relationships between shell and flesh weights in *Mytilus* populations experiencing different degrees of aerial exposure and briefly comments on the possible importance of such considerations to studies of foraging behaviour in those predators that are known to feed extensively on sea mussels.

Table 1

Variations in Shell Weight in *Mytilus edulis*

Shell Length (cm)	Shell weight (g)					
	ⁱ High shore Filey Brigg	ⁱ Low shore Filey Brigg	ⁱⁱⁱ High shore Filey Bay	^{iv} Low shore Filey Bay	^v High shore Robin Hood's Bay	^{vi} Low shore Whitby Harbour
1.50	0.20	0.16	0.25	0.21	0.21	0.19
2.50	0.98	0.83	1.30	0.85	1.09	0.85
3.50	3.45	2.57	4.49	2.31	—	2.73
4.50	—	—	7.93	5.01	—	5.81
5.50	—	—	11.45	7.87	—	10.71
6.50	—	—	—	—	—	18.80
n	432	373	490	360	71	102

Filey Brigg and Robin Hood's Bay are high energy, waveswept shores.

Filey Bay and Whitby Harbour are low energy, protected shores.

All sites situated on the North Sea coast of N.E. England.

RAO (1953) demonstrated that shell weight in both *Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837 decreased as exposure to air increased, the heaviest shells for any given flesh weight occurring amongst permanently submerged mussels. He attributed this relationship to the propensity of mussels for extracting calcium from seawater — thus the longer a mussel remained exposed to seawater the heavier its shell became. RAO (1953a) also noted an apparently similar phenomenon (though with somewhat different causes) in relation to high and low latitudinal mussel populations. FOX & COE (1943), however, found that *M. californianus* from the higher intertidal zone had thicker (and therefore presumably heavier) shells than conspecifics of similar length further down the shore, an observation which was subsequently corroborated by KOPP (1979) for *M. californianus* and by BAIRD & DRINNAN (1957) for *M. edulis*. Fast growing subtidal populations, by contrast, tend to have relatively thin rather brittle shells. BAIRD & DRINNAN (*op. cit.*) explained their findings in terms of requirements for basal metabolism. When mussels are exposed to air, basal metabolism reduces flesh weight at a greater rate than chemical erosion reduces the shell. Higher intertidal mussels will therefore have higher shell-flesh ratios than those from the lower intertidal zone. More recently, SEED (1973) obtained similar results for *M. edulis* from several contrasted localities. When mussels of similar shell length (though of differing age since growth rates also vary widely with intertidal height) were compared, those from the high shore had consistently heavier shell weights than those from the low shore (see also KOPP (1979) for *M. californianus*). Moreover, shell-flesh ratios generally increased with increasing shell length suggesting that as mussels age, their shells account for a progressively greater proportion of their total body weight. Figure 1 illustrates the relationship between shell and tissue weights as functions of intertidal height in mussels from 2 contrasted rocky shores on the NE coast of England. Mussels from the high shore consistently had heavier (= stronger) shells for any given weight of tissue than those from the low shore.

Although previous explanations for the observed differences in shell-flesh relationships amongst vertically separated mussel populations appear to have been sought in physiological terms, other possibly equally important factors such as longevity and population stability¹ ought perhaps also be considered. Stability and longevity in rocky shore mussel populations are known to increase

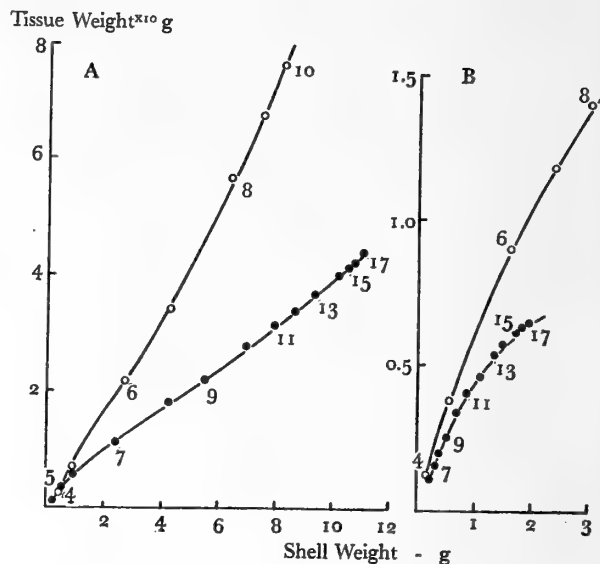


Figure 1

The relationship between shell and tissue weights as functions of intertidal height in mussels of known age and size from (A) Filey Bay — a comparatively low energy shore and (B) Filey Brigg — a severely wave exposed high energy shore. Solid symbols represent high shore populations; open symbols, low shore populations. Numbers indicate the estimated age of mussels of known size

progressively with increasing intertidal height (SEED, 1976; see also LEWIS, 1972). In the low shore, heavy settlement and rapid growth are generally accompanied by exceedingly intense predation resulting in a rapid turnover of mussels and wide oscillations in population density. By contrast, the higher intertidal area provides a spatial refuge largely free of mussel predators and although recruitment and growth are here substantially reduced, enhanced longevity confers considerable long term population stability. High shore populations are therefore frequently characterised by relatively high proportions of old, slow-growing mussels with typically high shell-flesh ratios. It is by no means unusual for many of these upper shore populations to consist of 20 or more year classes even though the largest mussels in such populations may measure only 2–3 cm in shell length (SEED, 1969).

On certain shores, however, mussels can also attain substantial immunity from predation by way of large body size, thereby surpassing the ability of any single predator to consume them (PAINE, 1976). This will be partly determined by local predation pressure but it will also be considerably enhanced in habitats which are optimal for

¹ I use the term 'stability' to denote the absence of any marked temporal change in population structure

mussel growth, *e. g.*, the low shore and subtidal regions. Size-limited predation may conceivably be more characteristic of *Mytilus californianus* populations since this species appears to be rather less attractive than *M. edulis* to certain predators, probably by virtue of its strong, heavily ribbed shell and its ability to grow to a much larger body size (HARGER, 1972). However, low shore populations of unusually large and sometimes apparently very old *M. edulis* are occasionally encountered, more especially in habitats sheltered from wave action where local growth rates may be substantially improved. Although these large bodied, apparently predator-free mussels will increase the stability and structural diversity of such populations thereby enabling both predator and prey to coexist in close proximity, their presence will also substantially alter the microenvironment available to newly recruited mussels. Small mussels which settle in amongst these larger individuals will experience severe intraspecific competition for food and their growth rates can therefore be greatly reduced (*e. g.*, SEED, 1969). At the same time, however, the matrix of large mussels will offer substantial protection from predators and many of these populations could therefore exhibit many of the characteristic features more generally associated with high shore mussel populations (*i. e.*, greater stability, enhanced longevity, and high shell-flesh ratios). Consideration of the structure and relative stability of mussel populations can therefore go some way towards explaining the apparently contradictory literature regarding shell-flesh relationships in mussels collected from different local habitats. It may therefore be relevant to note that the subtidal mussels (*M. edulis*) studied by RAO (1953) came from the underside of floats, a habitat in which mussels may be substantially protected against predation. More recently, size-limited predation has been demonstrated in subtidal *Modiolus modiolus* (Linnaeus) (SEED & BROWN, 1978) and these populations too exhibit considerable long term stability.

From this brief account it will perhaps be appreciated that sea mussels vary considerably in their shell-flesh characteristics according to the very local nature of both the physical and biological environment. Accordingly, the amount of time a predator might spend handling mussels of comparable size but different shell strength could vary within quite broad limits as indeed could the eventual food value yielded by such mussels. Furthermore, many of the common predators of sea mussels forage over relatively wide areas whilst some also exhibit regular tidal

and seasonal migrations. Since an extremely wide range of mussel types could therefore be encountered by these foraging predators, rigorous investigations of the size structure and shell-flesh characteristics of locally occurring mussel populations will clearly be fundamental to any proper understanding of the foraging behaviour of those predators known to utilise mussels as a major food resource.

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The Nudibranch *Aegires albopunctatus*

(Polyceratacea : Aegiretidae)

Preys on *Leucilla nuttingi*

(Porifera : Calcarea)

BY

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(1 Plate; 2 Text figures)

IT HAS BEEN CONSIDERED axiomatic that cryptobranchiate dorid nudibranchs (Doridacea or Eudoridacea) with simple or denticled hamate teeth are primarily sponge feeders (YOUNG, 1970) and that phanerobranchs (Polyceratacea) usually feed on bryozoans (*e. g.* MILLER, 1961).

A recent literature compilation for Californian nudibranchs (McDONALD & NYBAKKEN, 1978) has shown the known diet of numerous species; all 6 species of Polyceratacea (= Nonsuctoria) feed on bryozoans; 13 of the 14 cryptobranch species listed feed on various demospongiae (the exception, *Hallaxa chani* Gosliner & Williams, 1975, feeds on tunicates, and has a distinctly different radular morphology).

Radular morphology indicates prey specificity (BERTSCH, 1974): thus it is curious to find a sponge-

feeding radula type in a superfamily characteristically reported to feed on bryozoans. Within the Polyceratacea, species of *Aegires* Lovén, 1844, and *Notodoris* Bergh, 1875, have typical sponge-feeding radulae with simple, hamate teeth.

PRUVOT-FOL (1954: 245) commented on the similarity between radulae of the European *Aegires punctilucens* (Orbigny, 1837) and those possessed by other rasping sponge feeders: "La radula est banale, rapprochant cette famille des Archidoridinae . . . Tout semble indiquer que, malgré des divergences, les Aegirétidés doivent être rapprochés des Doridiens vrais, mangeurs d'éponges." Paradoxically, MILLER (1961: 106) suggests that *A. punctilucens* feeds on bryozoans (*Membranipora* and *Electra*) and THOMPSON & BROWN (1976: 108) state its colora-

Explanation of Figures 1 to 4

Scanning Electron Micrographs of the Radula
of *Aegires albopunctatus*

SEMs by Robert Pettyjohn and Hans Bertsch

Figure 1: View of the entire radula.

× 60

Figure 2: Outermost teeth of the anterior 6 rows. A basal flange is clearly visible on the inner side of the teeth (providing within-row structural support). The overlapping rows pro-

vide between-row strengthening. BERTSCH *et al.* (1973: 292) comment on similar aspects of radular functional morphology in the Chromodorididae (cryptobranchiate sponge-feeding dorids). × 300

Figure 3: Central part of the radula showing naked rachidian region and the smaller size of the innermost 4 or 5 teeth.

× 420

Figure 4: Posterior region of the radula; note the thin, developing innermost teeth.

× 300



Figure 1

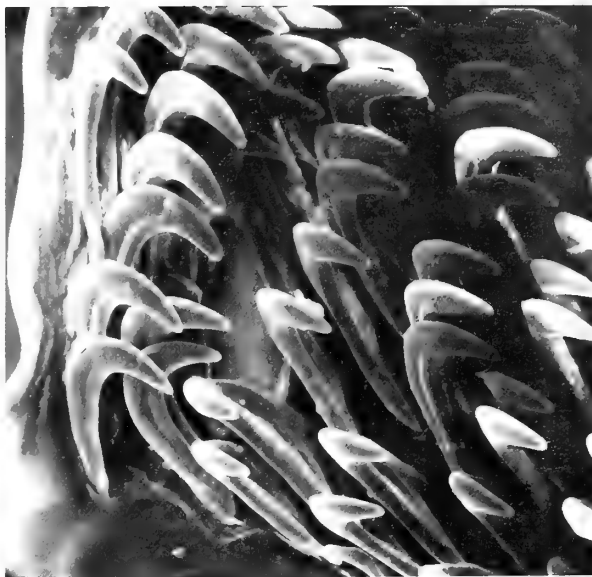


Figure 2

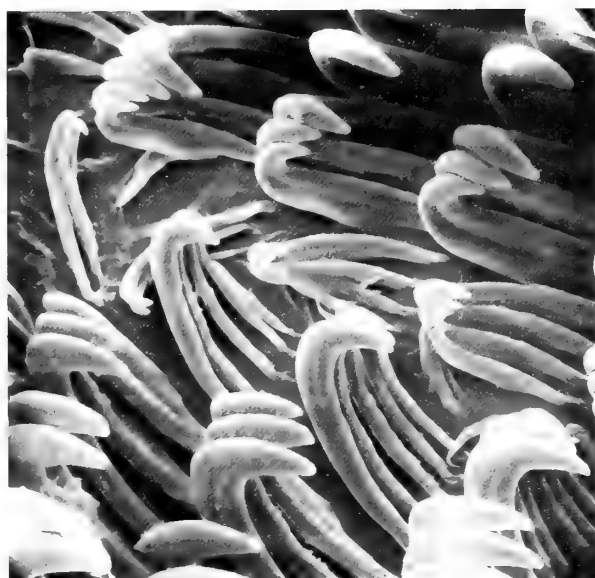


Figure 3



Figure 4

tion camouflages *A. punctilucens* to its prey item, "encrusting polyzoans."

Radulae of the California *Aegires albopunctatus* MacFarland, 1905, bear 15-22 rows of simple, hamate teeth (Figure 1). The morphology of these teeth (Figures 2 and 3) is similar to the radular teeth shape of known cryptobranch sponge feeders (compare with illustrations in FERREIRA & BERTSCH, 1975; BLOOM, 1976; BERTSCH, 1976; and throughout the opisthobranch literature). Newly forming teeth (Figures 1 and 4) are weak and thin. The teeth grow and thicken first on the outer portion of the posterior rows. The most recently formed teeth occur in the center of the developing rows (Figure 4).

MACFARLAND (1906: 133) reports that *Aegires albopunctatus* was "especially common upon sponges in a tunnel-like grotto formed by the waves near Pebble Beach, on Carmelo Bay" (Monterey, California), and RICKETTS & CALVIN (1968: 107) state that *A. albopunctatus* can be found on a "harmless variety" of white sponge. Except for these 2 obscure statements, there is no other published mention of a food source for *A. albopunctatus*.

On 21 April 1979, while leading several teams of scuba divers underwater, I found 9 specimens of *Aegires albopunctatus* (8-19 mm in total length, $\bar{x} = 12.3$ mm). Some were preying on the sponge *Leucilla nuttingi* (Urban, 1902). Five of the nudibranchs were in the

midst of different colonies of *L. nuttingi* (Figure 5). Clearly visible were sponges with pieces chewed out by the nudibranchs (Figure 6). These preliminary observations were made during a 25-minute timed search, on a 50 foot (15 m) dive, in the kelp beds off Point Loma (San Diego, California), northwest of the Cabrillo Lighthouse.

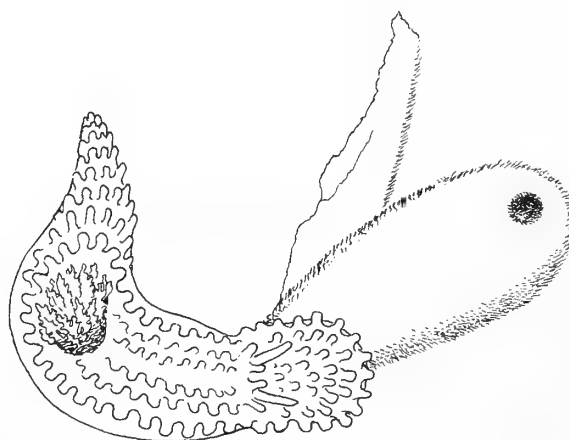


Figure 6

Aegires and *Leucilla*; the upper sponge has had $\frac{3}{4}$ of its width eaten away by *Aegires*, leaving only a thin piece of the normally inflated-tube-shaped sponge.

Drawing by Anthony D'Attilio, based on underwater photographs taken *in situ*, in the Point Loma kelp beds off San Diego, California

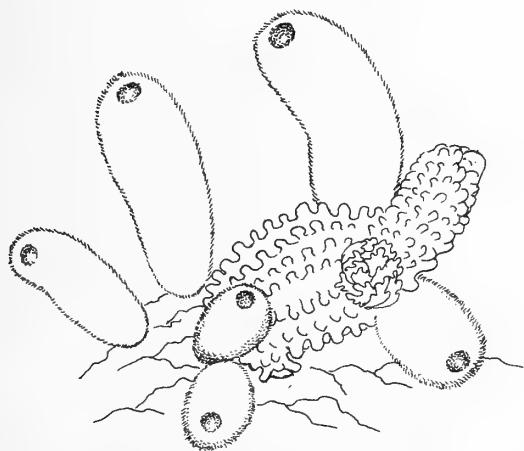


Figure 5

The nudibranch *Aegires albopunctatus*, crawling in the midst of a colony of *Leucilla nuttingi*. The nudibranch is 16 mm long. Drawing by Anthony D'Attilio, based on underwater photographs taken *in situ*, in the Point Loma kelp beds off San Diego, California

To survey the association of *Aegires* and *Leucilla*, I returned to the Point Loma kelp beds with 5 pairs of scuba diving teams, on the morning of 11 May 1979. We measured every *A. albopunctatus* found, counted all colonies of *L. nuttingi*, and measured the proximity of the 2 organisms. Diving depths varied from 40-55 feet (12-17 m); total underwater search time of the teams was 3 hours and 16 minutes. This area was within 2 km of the original location.

We found 25 *Aegires albopunctatus* (Table 1), of which 76% were either touching or less than 30 cm away from a *Leucilla* colony. The nudibranchs varied in total length from 4 mm to 20 mm ($\bar{x} = 10.4$ mm). Of the *L. nuttingi* colonies counted, 26% were associated with the nudibranch predator (on the colony or less than 30 cm distant).

The habitat studied was a smooth rock substrate, with periodic sandy areas, in the midst of the kelp beds. Other

Table 1

Subtidal survey of *Aegires albopunctatus*
and *Leucilla nuttingi*

Total <i>Leucilla nuttingi</i> colonies	74
Total <i>Aegires albopunctatus</i>	25
Number of <i>Aegires</i> directly touching <i>Leucilla</i>	10
Number of <i>Aegires</i> \leq 30 cm from <i>Leucilla</i>	9
<i>Aegires</i> with no proximate sponge	6

molluscan species common in the area included the prosobranchs *Haliotis* spp., *Mitra idae* Melvill, 1893, *Kelletia kelletii* (Forbes, 1852), and the nudibranchs *Cadlina flavomaculata* MacFarland, 1905, *Doriopsilla albopunctata* (Cooper, 1863), *Tritonia festiva* (Stearns, 1873), *Anisodoris nobilis* (MacFarland, 1905), and *Discodoris sandiegensis* (Cooper, 1863), and, more rarely, *Laila cockerelli* MacFarland, 1905, and *Archidoris odhneri* (MacFarland, 1966). The sea urchin, *Strongylocentrotus franciscanus* (Agassiz, 1863) and its commensal alpheid shrimp *Betaeus macginitieae* Hart, 1964, were also extremely common.

CONCLUSION

Aegires albopunctatus feeds on the calcareous sponge *Leucilla nuttingi*. Scuba divers have found 76% of the *A. albopunctatus* associated with (or in the close proximity of) this sponge subtidally in May. Further studies are required to determine whether there is any seasonal variation in the predator-prey relationship between *A. albopunctatus* and *L. nuttingi*, or whether *Aegires* is monophagous. The phylogenetic relationships and superfamilial placement of the Aegiretidae need additional investigation.

ACKNOWLEDGMENTS

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Karyotypes of Six Eastern Pacific Acmaeid Gastropods

BY

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(1 Plate; 4 Text figures)

INTRODUCTION

INTERTIDAL LIMPETS OF THE FAMILY Acmaeidae are globally widespread and particularly well represented in the Eastern Pacific, where at least 24 species can be found from Baja California to Alaska. Among these many have widely overlapping ranges and sympatric associations of five or more are not uncommon.

The systematics of the Acmaeidae have been extensively studied by TEST (1938) and McLEAN (1966). Test based her arrangements mainly on radular ribbon characteristics, McLean on both radular teeth characteristics and shell morphology. The two studies are in close agreement as to their designations of species but differ substantially in their generic and subgeneric groupings. Test included all but one species (*Lottia gigantea* Sowerby, 1834) in the one genus *Acmaea*. But McLean (1966), whose arrangement is currently accepted, divides the Eastern Pacific species into three genera: *Acmaea*, *Collisella*, and *Lottia*. McLean now (1969) regards his subgenera of *Collisella*, *C.* (*Collisella*) and *C.* (*Notoacmea*), as full genera.

Karyotypes provide another taxonomic character to consider in the systematics of any species group, and it is the intention of this study to contribute cytotaxonomic evidence to Acmaeid systematics. Here, the karyotypes of 3 members each from *Notoacmea* and *Collisella* are presented: *N. scutum* (Rathke, 1833), *N. fenestrata* (Reeve, 1855), *N. persona* (Rathke, 1833), *C. digitalis* (Rathke, 1833), *C. pelta* (Rathke, 1833), and *C. strigatella* (Carpenter, 1864). Chromosome number, size, and centromere position are the karyotypic characteristics examined.

The only other cytotaxonomic study of the Acmaeidae (see PATTERSON, 1969, for the most recent review of molluscan chromosomes) was that of NISHIKAWA (1962) on 6 Japanese limpets. Three of these he classified in the genus *Notoacmea*: *N. schrenckii* (Lishke, 1868), *N. concinna*

(Lishke, 1870), and *N. fuscoviridis* Teramachi (1949); and 3 in the genus *Patelloida*: *P. saccharina lanx* (Reeve, 1855), *P. pygmaea* (Dunker, 1860), and *P. lampanicola* Habe (1944). In all of these species, and in 3 species of the closely related family Patellidae (both are in the superfamily Patelloacea), he found a consistent haploid number of 9. Although details of chromosome morphology are lacking from Nishikawa's study, his findings provide an opportunity to compare chromosome counts of Western Pacific Acmaeids to those of the Eastern Pacific.

MATERIALS AND METHODS

Limpets of the 6 species of Acmaeidae examined in this study were collected from rocky intertidal habitats along the central Oregon coast, between Yachats on the south and Neskowin on the north. Only those individuals that could be clearly classified as to species (according to the keys of LIGHT *et al.* (1975), KOZLOFF (1974) and McLEAN (1969)) were used. The animals were kept in a running saltwater facility at the Oregon State University campus until they were ready to be examined for karyotypes.

Two methods were used to obtain karyotypes of these 6 species: the first employed colchicine arrested metaphase I spermatocyte nuclei; the second, cultured embryos, which yielded mitotic cleavage nuclei.

Spermatocytes were obtained by first injecting 0.2 mL of 0.5% colchicine into the body cavity (to enrich the recovery of metaphase nuclei), by dissecting out the testis two hours later, and then submitting the testis for about 15 min. to a hypotonic 1% Na₂citrate solution to swell the nuclei. Testes were subsequently macerated, fixed in freshly made Carnoy's solution (3 prts. 100% ETOH: 1 prt. glacial acetic acid) for 2 h, and stained for 5 min. on a siliconized glass slide with 1% lactic-acetic orcein. Stain-

ing was followed by rather vigorous squashing under a cover slip. With this technique, only highly condensed metaphase I nuclei could be observed (Figure 1), useful for chromosome counts but unsuitable for any characterization of chromosome morphology.

With cultured embryos, however, large numbers of mitotic metaphases could be obtained, showing both chromosome number and karyotypic details of chromosome size and centromere position (Figure 3). Fertilization was carried out following the procedure reported by STRATHMAN (1975). Embryos were subjected to a colchicine treatment during the last five hours of culture (4 mL of 0.5% colchicine per 200 mL sea water), which markedly increased the number of metaphase nuclei in embryos beyond the 32 cell stage. Unfertilized embryos were usually arrested at late diplotene, and thus were useful for confirming chromosome counts (Figure 2).

At the end of the culture period the embryos were put in a hypotonic solution (1 prt. sea water: 2 prts. distilled water) to swell the nuclei and then fixed for several hours in fresh Carnoy's. The fixed embryos were treated overnight in a 1 part chloroform: 1 part ethanol/methanol solution to extract the yolk and then stored in 70% ethanol. Mitotic nuclei from these embryos were obtained by staining a few embryos on a siliconized glass slide with 1% lactic-acetic orcein for 5 to 10 min. and then squashing them under a siliconized cover slip with light to moderate pressure. Broken nuclei were often mixed making chromosome counts difficult, but this was less of a problem with more mature embryos. Only discrete, well-separated nuclei were used to establish karyotypes.

Photographs (such as Figure 3) proved inadequate for a clear characterization of karyotype; consequently, camera lucida drawings were made with a Zeiss phase contrast microscope using a 25X ocular and a 100X objective (Figures 5 and 6).

To obtain the karyotypes, drawings of individual chromosomes were measured to the nearest half millimeter, the lengths of the 2 short arms (S) and 2 long arms (L) were each averaged, and with these two values the arm ratio ($R = L/S$) and % of total genome

($\% = \frac{L_1 + S_1}{L_n + S_n}(100)$) were calculated. From these values individual chromosomes were plotted (R vs. % of total genome) to distinguish pairing relationships (Figure 4a). From 3 such karyotypes (one from each of 3 separately fertilized cultures) a pattern of matched chromosome pairs was determined (Figure 4b). Although there was some scatter within a chromosome pair of a sample karyotype and for each chromosome pair of a species karyotype, a definite clustering of pairs from the sample karyotypes permitted determination of the species karyotype. In some cases (e.g. chromosome pairs 6 and 8, Figure 4a) where alternative pairing relationships were reasonably possible for a sample karyotype, the pairing which was used was the one most consistent with the other sample karyotypes for that species. Distortion during squashing most likely accounts for the scatter within a chromosome pair, but possible intraspecific chromosomal variation within the limits of the scatter was not resolvable.

To summarize, from three separately fertilized embryos of each species the average size (% of total genome) and centromere position (R value) for particular chromosome pairs were determined. The karyotype of each species is the series of chromosomes, in order of ascending size, characterized by these values.

RESULTS AND OBSERVATIONS

For all six species the modal number of chromosomes in mitotic cleavage nuclei was $2n=20$. This number was found in virtually all discrete yet well spread nuclei examined, and was substantiated by a haploid count of 10 made in several metaphase I spermatocytes (Figure 1) or unfertilized oocytes (Figure 2) for each species. Although these animals have separate sexes, no typical sex chromosome characteristics (such as heteromorphic pairs or differential staining of any elements) were observed.

Quantified karyotypic data (% of total genome and R values) of both the sample and species karyotypes are presented in Table 1. Comparative karyotypes of camera lu-

Explanation of Figures 1 to 3

Figure 1: Photographs of 2 metaphase I spermatocyte nuclei (squash preparations) from *Collisella digitalis*. Ten bivalents are clearly visible in each photograph $\times 625$

Figure 2: Photograph of late diplotene oocyte nucleus (squash preparation) from *Notoacmea fenestrata*. Ten bivalents visible $\times 250$

Figure 3: Photograph of colchicine metaphase nucleus from cleaving embryo of *Notoacmea scutum*. $2n=20$ $\times 250$

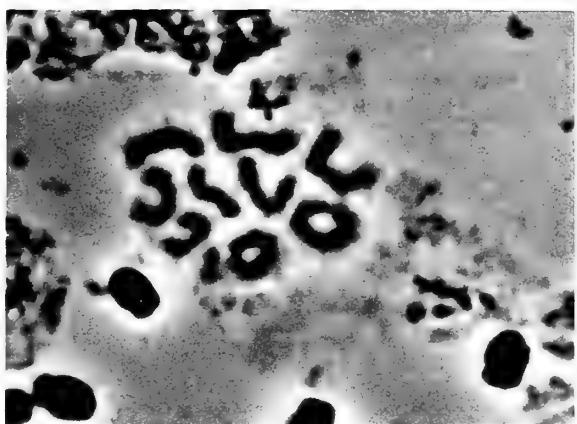


Figure 1a



Figure 1b

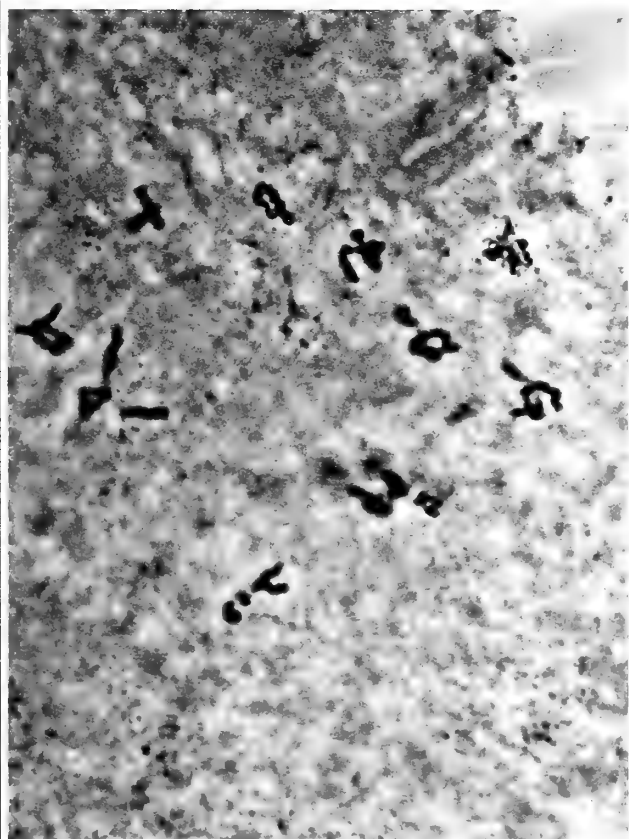


Figure 2

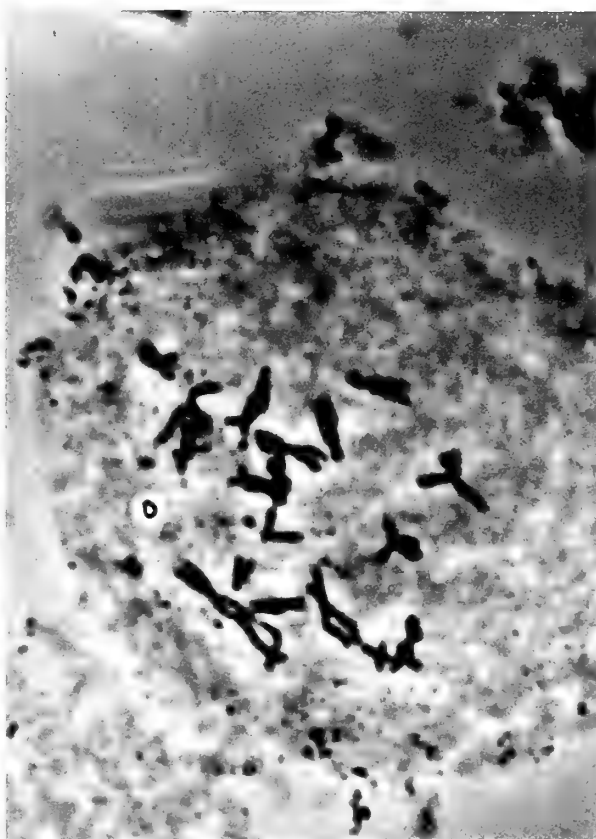


Figure 3

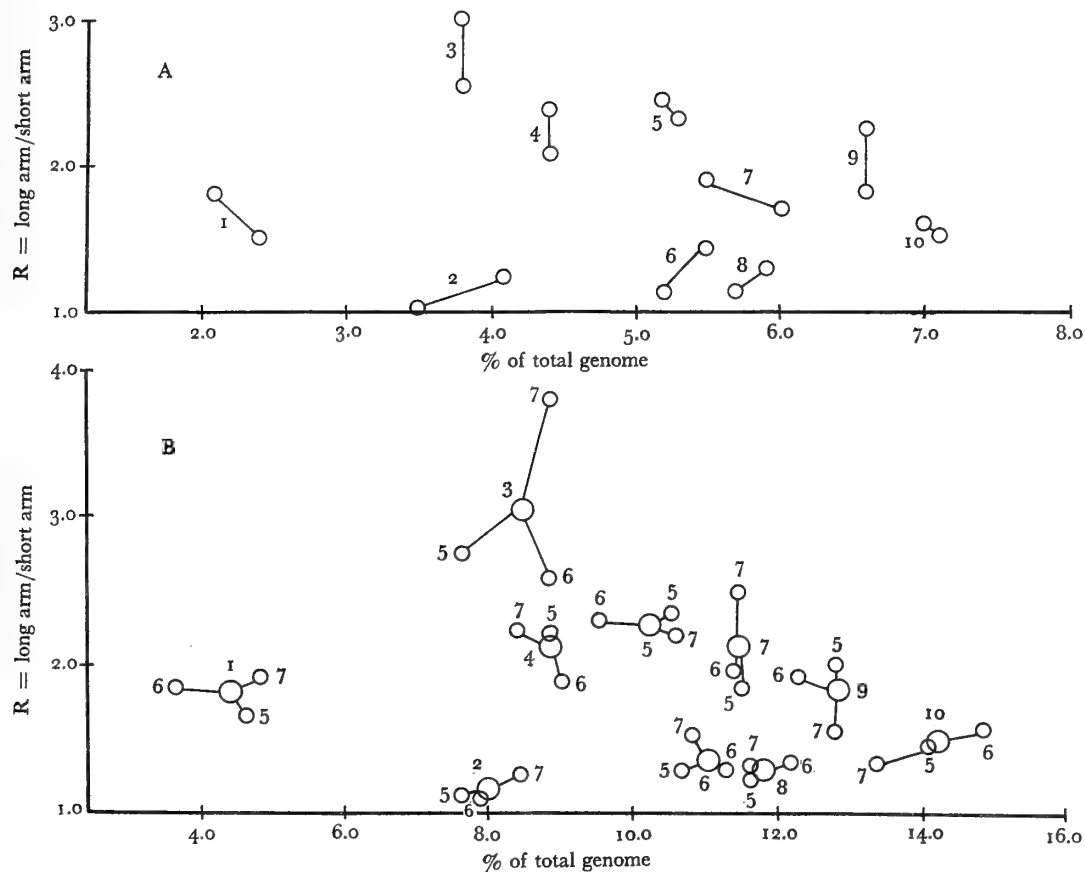


Figure 4

a) Individual mitotic chromosomes from one metaphase cleavage nucleus of *Collisella digitalis* plotted as R vs. % of total genome. Numbers designate chromosome pairs.

b) Graph of chromosome pair values (small circles) for R and % of total genome from 3 nuclei of *Collisella digitalis* and of their

mean values (large circles). Pair values for each sample determined from mean of individual homolog values. Mean values for R and % of total genome from 3 samples characterize species karyotype. Small numbers refer to samples 5, 6, and 7, and large numbers designate chromosome pair number

cida drawn chromosomes can be seen in Figure 6, and an idiogram for the karyotype of *Collisella digitalis*, constructed from the data in Table 1, is shown in Figure 7.

Certain aspects of these data need comment. Firstly, chromosome pairs 3 and 4 were not consistently distinguishable in *Notoacmea persona* and *N. fenestrata*; hence, they were averaged. Secondly, in the karyotypes of both *Collisella strigatella* and *N. scutum* pair 6 is out of size order. In each case 2 of the 3 samples warranted the size order designated in the karyotypes, and the centromere

positions of that chromosome for all 3 samples of the 2 species were close to those of chromosome 6 from the other 4 species. Putting these 2 chromosomes of anomalous size in any other order would indicate karyotypic differences that may not be real. But because of these and other variations among the samples of a species karyotype, the resolution of this method of determining karyotypic differences between species is somewhat reduced. If we err, we err on the side of a conservative estimate of the amount of chromosomal rearrangement in the Acmaeidae.

Table 1

Size and arm ratios of chromosome pairs from sample and species karyotypes of six Eastern Pacific Acmaeidae.

Sample	Species no. or mean of samples	Chromosome number																			
		1		2		3		4		5		6		7		8		9		10	
		R	CP	R	CP	R	CP	R	CP	R	CP	R	CP	R	CP	R	CP	R	CP	R	CP
<i>Notocmea</i>	3	4.4	2.38	8.3	3.17	8.3	2.03	9.1	2.75	9.6	2.94	10.0	1.26	10.7	1.48	12.6	1.66	12.8	1.47	14.0	1.55
<i>scutum</i>	7	5.0	1.41	6.4	4.59	8.5	2.79	9.8	2.73	10.2	2.84	7.5	1.37	10.1	1.27	12.9	2.41	12.9	1.53	14.2	1.24
	8	4.9	1.63	6.2	3.50	8.4	2.62	9.0	4.50	9.2	2.45	9.9	1.68	11.3	1.65	12.8	2.82	13.6	1.48	14.5	1.95
	mean	4.8	1.81 sm	7.0	3.75 st	8.4	2.48 sm	9.4	3.33 st	9.7	2.74 sm	9.1	1.44 m	10.7	1.47 m	12.8	2.30 sm	13.1	1.49 m	14.2	1.58 m
<i>Notocmea</i>	5	4.5	1.54	6.8	3.64	8.9	2.22			9.5	1.25	10.6	1.52	12.3	1.29	12.4	2.00	13.1	1.13	13.3	1.65
<i>fenestrala</i>	6	4.8	1.93	7.2	4.14	9.2	2.11			10.1	1.16	11.8	1.82	11.5	1.25	12.3	1.75	12.3	1.16	13.4	1.89
	7	4.5	2.43	6.3	3.38	8.2	2.03			8.7	1.20	11.2	1.74	12.0	1.20	12.1	1.48	13.8	1.13	15.3	1.99
	mean	4.6	1.97 sm	6.8	3.72 st	8.8	2.12 sm			9.4	1.20 m	11.2	1.69 m	11.9	1.25 m	12.3	1.74 sm	13.1	1.14 m	14.0	1.84 sm
<i>Notocmea</i>	7	3.4	1.76	6.4	2.90	8.8	1.93			10.6	1.71	10.3	1.19	11.2	1.15	12.8	2.71	12.6	1.39	14.4	1.57
<i>persona</i>	9	4.4	1.74	6.4	2.33	8.4	2.04			9.4	2.03	11.2	1.49	12.0	1.39	11.4	2.84	12.7	1.17	15.6	1.57
	10	4.4	1.78	6.6	2.61	8.2	2.36			9.4	2.24	10.4	1.09	11.5	1.23	12.8	2.95	13.6	1.36	15.6	1.24
	mean	4.1	1.76 sm	6.5	2.61 sm	8.5	2.11 sm			9.8	1.99 sm	10.6	1.26 m	11.6	1.26 m	12.3	2.83 sm	13.0	1.31 m	15.2	1.36 m
<i>Collisella</i>	8	5.0	2.23	7.9	2.08	9.2	3.63	8.3	2.65	9.6	2.06	10.8	1.13	10.3	1.51	12.1	1.09	11.7	1.88	16.1	1.56
<i>pella</i>	9	3.5	2.07	8.1	2.25	8.3	3.09	9.2	2.42	9.5	2.16	11.0	1.20	11.3	2.03	12.7	1.30	12.8	1.88	14.6	1.26
	10	3.4	1.77	7.7	2.68	8.2	3.40	8.7	2.90	9.7	1.98	10.8	1.16	10.7	2.03	12.3	1.12	13.0	1.56	15.0	1.77
	mean	4.0	2.02 sm	7.9	2.34 sm	8.6	3.37 st	8.7	2.66 sm	9.6	2.07 sm	10.9	1.16 m	10.8	1.86 sm	12.4	1.17 m	12.5	1.77 sm	15.2	1.53 m
<i>Collisella</i>	5	4.5	1.66	7.6	1.14	7.6	2.78	8.8	2.25	10.5	2.38	10.7	1.29	11.5	1.86	11.6	1.23	13.2	2.04	14.1	1.51
<i>digitilis</i>	6	3.6	1.82	7.9	1.12	8.8	2.60	9.0	1.91	9.5	2.33	11.3	1.31	11.4	2.56	12.2	1.36	12.3	1.96	14.9	1.60
	7	4.8	1.91	8.4	1.26	8.8	3.85	8.4	2.26	10.6	2.22	10.8	1.53	11.4	1.99	11.6	1.30	12.8	1.57	13.4	1.35
	mean	4.3	1.80 sm	8.0	1.17 m	8.4	3.08 st	8.7	2.14 sm	10.2	2.31 sm	10.9	1.38 m	11.4	2.14 sm	11.8	1.30 m	12.8	1.86 sm	14.1	1.51 m
<i>Collisella</i>	5	4.8	2.21	7.5	2.24	8.1	2.67	9.1	2.96	10.0	2.64	9.9	1.22	11.5	1.12	11.0	1.55	13.2	1.64	14.8	1.70
<i>strigatella</i>	6	4.0	2.21	7.7	1.92	8.7	3.20	9.3	3.19	10.3	2.11	7.8	1.12	11.0	1.17	11.9	1.45	13.1	1.27	16.2	1.71
	8	4.4	1.98	8.0	3.11	9.2	3.58	10.3	3.95	9.8	2.81	9.6	1.27	10.2	1.28	11.6	1.70	12.1	1.38	14.8	1.31
	mean	4.4	2.13 sm	7.7	2.42 sm	8.7	3.15 st	9.6	3.37 st	10.0	2.52 sm	9.1	1.20 m	10.9	1.19 m	11.5	1.57 m	12.8	1.43 m	15.3	1.57 m

% = % of total genome

R = long arm length/short arm length

CP = centromere position

mean sample values = species karyotype values

m = median region ($1.0 < R < 1.7$)sm = submedian region ($1.7 < R < 3.0$)st = subterminal region ($3.0 < R < 7$)

The karyotypes of these six species show several general similarities. The range in size is fairly consistent among all the karyotypes: one very small chromosome comprising 4 to 5% of the total genome length (about $2\ \mu\text{m}$ to $3\ \mu\text{m}$; see scale in Figures 5 and 6) with the other 9 chromosomes in a more or less continuously ascending series of size up to 14 to 16% of the total genome length (about $9\ \mu\text{m}$ to $10\ \mu\text{m}$). Centromere position is generally median to submedian, with no pairs having terminal centromeres. Overall, the larger chromosomes have more median centromeres than the smaller ones.

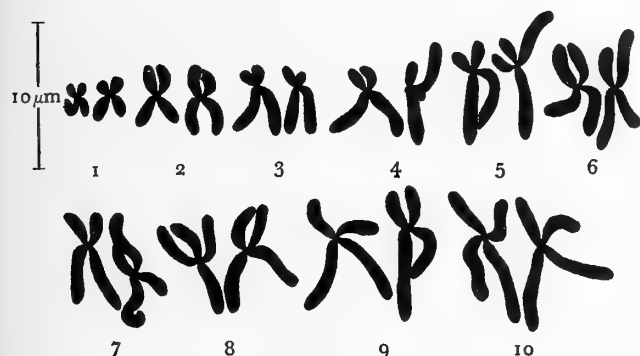


Figure 5

Camera lucida drawings of chromosomes paired from graph in Figure 4a (*Collisella digitalis*, sample 5)

In a comparison of the chromosomes of equivalent size among the 6 species, few marked changes in centromere position are observed. In *Notoacmea fenestrata* the centromere of chromosome 5 has a more median position than those of the equivalent chromosomes from the other species. *Notoacmea persona* has a noticeably more terminal centromere position for chromosome 8 than do the other species. *Collisella digitalis* shows two differences in comparison to the other species, one of these shared by *C. pelta*. Chromosome 2 of *C. digitalis* has a distinctly median centromere in contrast to the sub-median to sub-terminal centromere of no. 2 in the other 5 species. Chromosome 7 of both *C. digitalis* and *C. pelta* is more sub-median in centromere position than the median no. 7 of the other species.

Centromere shifts may occur by pericentric inversion (by 2 breaks) or by the rarer transposition of the centromere containing segment into another part of the chromosome (3 breaks required). The few centromere shifts re-

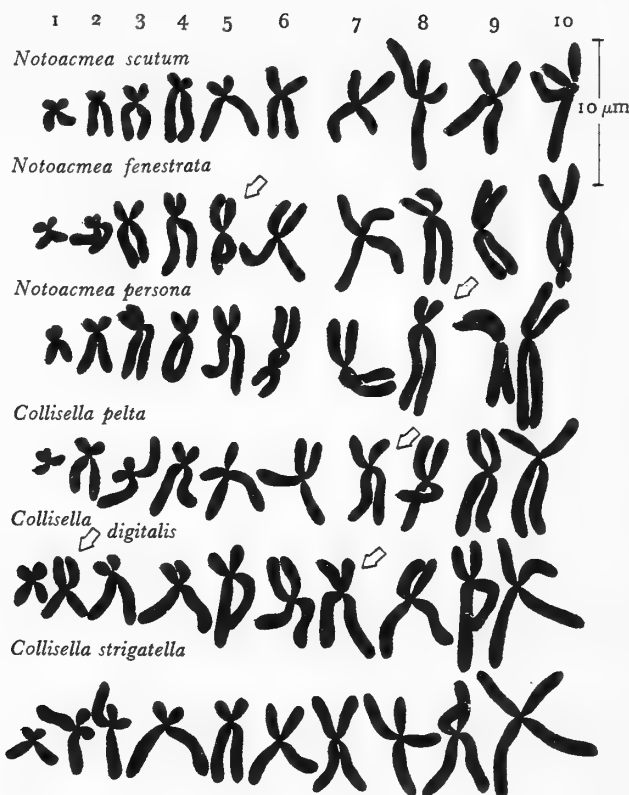


Figure 6

Karyotypes of 6 acmaeid species examined in this study. Only 1 chromosome per pair is presented ($n = 10$). All chromosomes in each karyotype are camera lucida drawings from 1 sample nucleus. Arrows indicate karyotypic differences discussed in text

corded may be due to a modest number of pericentric inversions fixed in the course of speciation of these limpets.

One might make the criticism that due to size variation among the samples comprising each species karyotype, designated chromosome numbers may not reflect the same homologous pair throughout the 6 species; consequently, the differences just pointed out may be accounted for by changes in the designation of chromosome number. But after making any reasonable rearrangements in size order within a karyotype, these reported differences represent a minimum estimate of karyotypic change among the 6 species.

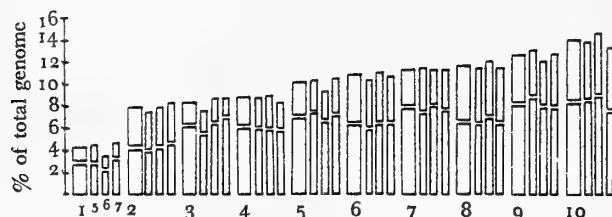


Figure 7

Idiograms of species karyotype (thick chromosomes) and sample karyotypes (thin chromosomes) for *Collisella digitalis*. Small numbers below chromosomes (5, 6, and 7) indicate order of sample karyotypes in idiogram. Idiograms were constructed from R (long arm length/short arm length) and % of total genome values for *Collisella digitalis* presented in Table 1 and Figure 4b

DISCUSSION

It appears from these data that speciation of Acmaeid gastropods has not been accompanied by extensive chromosomal rearrangement. Nevertheless, it must be kept in mind that rearrangements that do not visibly alter chromosome length or centromere position (e.g. symmetric pericentric inversions or paracentric inversions) may be present in these species.

Although genomic reorganization at the level of detectable karyotypic differences can sometimes act as a genetic isolating mechanism through the promotion of hybrid sterility or inviability (WHITE, 1973), the present results indicate that chromosomal rearrangements are not likely to play an important role in the reproductive isolation of sympatric Acmaeids. The question of the nature of isolating mechanisms remains open, although Fritchman's study of Acmaeid reproductive periods suggests that non-coincident spawning stimuli could in some cases result in reproductive isolation of sympatric limpets (FRITCHMAN, 1961a, 1961b, 1961c, 1962).

There is a paucity of comparative karyotypic data reported so far on gastropod species (see PATTERSON, 1969, for review), but a study by BURCH (1967) on the Japanese melaniid genus *Semisulcospira* shows that the Gastropoda are not all as karyotypically conservative as the Acmaeidae. Burch reported variations in chromosome number from $n=7$ to $n=20$ among the *Semisulcospira* species examined and numerous differences in centromere position in the karyotypes of those species with the same number of chromosomes.

Although few differences in karyotype among the Eastern Pacific Acmaeidae were found here, the difference in

chromosome number between these 6 Eastern Pacific species ($n=10$) and the 6 Western Pacific Acmaeidae ($n=9$) examined by NISHIKAWA (1962) is striking.

A change of one in chromosome number can be brought about by either a dissociation or fusion. Although the precise mechanisms are not well understood, a dissociation can be thought of as the division of a metacentric chromosome into two acrocentrics and a fusion as the joining of two acrocentrics into a metacentric, a process sometimes called Robertsonian translocation. It is not clear which of these two events is more likely to occur; therefore, one can not say whether $n=9$ or $n=10$ is the more primitive condition in the Acmaeidae.

The difference in chromosome number between the Eastern and Western Pacific Acmaeidae does, however, indicate that the species of Nishikawa's study and those analyzed here may represent separate phylogenetic groups: one $n=9$ group, including 3 species of *Patelloida* (*P. saccharina lanx*, *P. pygmaea*, *P. lampanicola*) and 3 species of *Notoacmea* (*N. schrenckii*, *N. concinna*, *N. fuscoviridis*); and a $n=10$ group, including 3 species of *Collisella* (*C. digitalis*, *C. pelta*, *C. strigatella*) and 3 species of *Notoacmea* (*N. scutum*, *N. persona*, *N. fenestrata*). But this presents a perplexing taxonomic situation if members of the same genus, *Notoacmea*, have members in each cytotaxonomically distinguishable group.

The present generic groupings of *Patelloida*, *Collisella*, and *Notoacmea* are based primarily on radular teeth characteristics: *Collisella* has uncini (rudimentary marginal teeth), *Notoacmea* lacks them, and *Patelloida* has two pairs of elongate marginal teeth (MCLEAN, 1966, 1969). No distinct shell differences among these 3 genera are evident, with the exception that no species of *Notoacmea* possesses heavy radial ribbing, whereas some species of *Collisella* and *Patelloida* are heavily ribbed. (The genus *Acmaea* is clearly distinguishable from the other Acmaeid genera by both shell and radular teeth characters (MCLEAN, 1966).) Based mainly on the one morphological criterion of radular teeth characteristics, these classifications would seem to be unambiguous. But reliance on primarily one characteristic (radular teeth) for classification may be less than adequate if the taxonomy of a species group is to reflect its phyletic relationships. Because a misrepresentation of the phylogenetic history of the Acmaeidae can only confuse further evolutionary studies, it is important to determine whether the cytotaxonomic evidence warrants a reexamination of Acmaeid systematics.

It is possible that NISHIKAWA's cytological technique (1962) failed to reveal a small chromosome (for example chromosome 1) common to the karyotypes of all 6 species in this study. Although Nishikawa's data are presented

only as camera lucida drawings of metaphase I spermatocyte nuclei, the clarity of his drawings and the fact that all of the metaphase I spermatocyte chromosomes of the species examined by us are darkly stained and distinct (Figure 1) make it unlikely that Nishikawa miscounted in all 6 species from the Western Pacific. Since the chromosome counts of the Eastern Pacific Acmaeidae reported here are well substantiated, it appears that there is a fundamental discrepancy between taxonomic classifications based on morphological criteria and the chromosomal evidence.

Although Test's groupings (subgeneric) based on radular ribbon criteria differ substantially from McLean's (generic), her arrangement of the species included in Nishikawa's and the present study is also found to be contradictory to the cytotaxonomic data.

In light of the inconsistencies between the classification based primarily on the single morphological criterion of radular teeth and the karyotypic data, it would seem desirable to confirm Nishikawa's results and to examine more anatomical and physiological characteristics of this group. Differences in enzyme electrophoretic patterns or hybrid viability studies could reveal phyletic groupings; and karyoptic studies (at least of chromosome number) need to be extended to more species for a more complete picture of cytotaxonomic groupings in the Acmaeidae. Perhaps, too, the phylogenetic significance of radular characteristics needs to be reevaluated. With these and other approaches possible, taxonomic work on the Acmaeidae certainly deserves more attention, for an adequate understanding of the interesting and complex evolutionary history of this family has yet to be achieved.

SUMMARY

1. Chromosome numbers in 3 species of *Notoacmea* (*N. scutum*, *N. persona*, *N. fenestrata*) and 3 species of *Collisella* (*C. pelta*, *C. digitalis*, *C. strigatella*), all found along the Pacific coast of temperate North America, were determined to be $n=10$ in each case.
2. Few differences in chromosome size or centromere position were observed among any of the 6 species karyotypes determined in this study. *Collisella pelta*, *Notoacmea persona*, *N. fenestrata* all show one clear change in centromere position and *C. digitalis* shows 2.
3. The count of $n=10$ differs from that of $n=9$ reported by Nishikawa (1962) for 3 species of *Notoacmea* and

3 species of *Patelloida* (also in the Acmaeidae) from the Western Pacific. In light of these differences, current taxonomic groupings of the Western and Eastern Pacific *Notoacmea* should be reevaluated.

ACKNOWLEDGMENTS

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The Distribution of Shallow-Water Marine Prosobranch Gastropod Molluscs Along the Coastline of Western Australia

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(5 Text figures)

INTRODUCTION

THE STATE OF WESTERN AUSTRALIA is the largest of the Australian States, occupying fully a third of the Australian continent. The coastline of the State is vast, about 7 000 km long, and has a wide variety of habitats. The coast spans some 21° of latitude (14° to 35° S) and 15° of longitude (114° to 129° E). This western portion of Australia was regarded as a wasteland by the early settlers who bypassed it on their way to the east coast. As the process of exploring and settling the eastern states continued, scientific knowledge of the fauna there surged ahead. With no population and little exploration in the west, the study of the fauna of Western Australia lagged behind. The first settlement in Western Australia was founded in Albany in 1827. By that time Sydney was already a thriving town and the Australian Museum was being established.

The early history of the scientific exploration of the Western Australian coastline was summarized by Hedley (1916), who compiled the published descriptions of Western Australian molluscs and found that about 800 species had been recorded in the State to that time. Of these about 550 were marine gastropods. While many of the species have since been synonymized or transferred to



(adjacent column →)

Figure 1

Map of Western Australia showing the locations of points mentioned in the text

other genera, Hedley's compilation is still the most extensive listing of Western Australian molluscs. HEDLEY (1926) later published an analysis of the zoogeography of Australian marine molluscs, but the species ranges in Western Australia were poorly known at that time. Many collections have been made in the intervening 74 years and the details of the distributional patterns of marine gastropods along the Western Australian coastlines can now be elucidated.

MATERIALS AND METHODS

The distributions in Western Australia of 440 species of prosobranch gastropods were established by analyzing the collections of the Western Australian Museum (WAM). CATE (1964; 1968) and WILSON & GILLET (1971) also used the WAM collections but had access to private collections which extended the known ranges of some species

beyond that recorded in the Museum holdings; the extended ranges have been used in this analysis. The 20 families selected for analysis are those that are best represented in the collection and are well known taxonomically. Table I lists the 20 families and the number of species examined in each; Appendix I lists the species examined and their ranges. The analysis provides a good coverage of the three prosobranch orders: 72 archeogastropods, 119 mesogastropods, and 249 neogastropods are discussed. This encompasses most of the prosobranchs whose range can be established with the WAM collections and the results can be considered to be representative.

The WAM collections are the result of an intensive field collecting programme conducted throughout the State during the last 14 years. Only material from the intertidal or the shallow depths that can be reached by SCUBA techniques, is analyzed in this paper. The overall outlines of the distributions of shallow-water prosobranchs can be established, but not every species has been collected at all of the major localities. In the case of widespread tropical Indo-Pacific or warm temperate southern Australian species the lack of a specimen from a particular locality in the middle of its range is considered to be an artifact and the ranges discussed assume the species will be recorded later at intermediate localities. This generalization of species ranges might obscure areas along the coast where groups of species are absent.

Table 1

Prosobranch families investigated in this paper.

Family	Number of species investigated
Archeogastropoda	
Haliotidae	10
Trochidae	37
Turbinidae	17
Neritidae	8
Mesogastropoda	
Littorinidae	9
Strombidae	15
Cypraeidae	61
Naticidae	14
Cassidae	14
Tonnidae	6
Neogastropoda	
Muricidae	26
Thaididae	22
Columbellidae	22
Fascioliariidae	13
Nassariidae	19
Olividae	9
Mitridae	51
Volutidae	23
Conidae	48
Terebridae	16
	440

RESULTS

Overall Patterns of Distribution

Three general distributional patterns emerge from the overall analysis of species distributions: the majority (308) of the species are widely distributed tropical species found in the Indo-Pacific region and along the tropical coasts of northern Australia, extending into Western Australia; a smaller group of 94 species are warm temperate forms distributed along the southern coast of Australia, including the south coast of W.A.; the smallest segment of the fauna is a group of 38 species that are endemic to Western Australia.

There are no major distributional features exhibited by the tropical species along the north coast (Figure 2). Of the 308 tropical species, 230 extend as far west as the North-West Cape-Barrow Island area. The 78 species that do not reach the North-West Cape area drop out gradually along the north coast. The North-West Cape area is the major geographical limit for the tropical fauna with

90 species having their range limits in the area. Two smaller areas of substantial range limits occur along the west coast at Shark Bay, where 43 species terminate, and the Houtman Abrolhos (47). Only 47 of the 308 tropical species extend south of the Houtman Abrolhos. These decrease gradually along the west coast until only 9 have been recorded at Cape Leeuwin at the southwestern corner of the State. Four tropical species (*Clanculus consorbinus*, *Cypraea caputserpentis*, *C. helvola*, and *Natica qualtieriana*) are found along the south coast to Albany. One species, *Natica sagittata*, is recorded as far as Esperance.

A similar, but reverse pattern, is exhibited by the warm temperate species (Figure 2). Eighty-eight of the 94 species are distributed along the entire south coast to Cape Leeuwin. Seventeen of these extend only to the Cape Leeuwin-Cape Naturaliste area. The major distribution limit for the warm temperate group is in the Perth area, which is the extreme range for 31 species. Forty of the southern species occur north of the Perth area, but 24 of these do not extend north of the Houtman Abrolhos-Geraldton area. The remaining 16 exhibit a gradual decline further north on the west coast, and only three extend to the north coast: *Nassarius particeps*, which extends to the Dampier Archipelago, and *Eunaticina dingeldi* and *Oliva australis*, both of which are found as far as Broome.

The distributions of the 38 species endemic to Western Australia are shown on Figure 2, and the species are listed on Table 2. Most occur only along the west coast though some extend to the north or south coast. The percentages of endemic species are about the same in the 3 prosobranch orders: 7.0% in the Archeogastropoda, 8.4% in the Mesogastropoda, and 9.2% among the Neogastropoda. None of the orders has a rate of endemism substantially different from the average rate of 8.6% endemic.

The presence of two overlapping faunas on the west coast provides an interesting area for the examination of the changes which occur in species populations near the extreme limit of their ranges. Figure 3 shows the relative percentages of northern and southern species along the west coast. There is a clear decline in the percentage of tropical species southward along the coast. The molluscan fauna of both North-West Cape and Shark Bay is almost completely tropical. The Abrolhos is 72% tropical. South of the Abrolhos the percentage of tropical species declines sharply, decreasing to 39% in the Perth area. The fauna of the southwest corner of the State is predominately warm temperate. The major overlap between the tropical and warm temperate faunas occurs on the stretch of coastline between Perth and the Houtman Abrolhos.

Table 2

Species investigated that are endemic to Western Australia.

Archeogastropoda
Haliotidae
<i>Haliotis elegans</i>
<i>H. semiplicata</i>
Trochidae
<i>Calliostoma ciliaris</i>
<i>C. lepidus</i>
<i>Clanculus occidus</i>
Mesogastropoda
Littorinidae
<i>Nodilittorina australis</i>
<i>N. nodosa</i>
<i>Tectarius rusticus</i>
Cypraeidae
<i>Cypraea armeniaca</i>
<i>C. brevidentata</i>
<i>C. decipiens</i>
<i>C. pulicaria</i>
<i>C. rosselli</i>
<i>C. venusta</i>
Cassidae
<i>Phalium whitworthi</i>
Neogastropoda
Muricidae
<i>Haustellum wilsoni</i>
<i>Pterynotus westralis</i>
<i>Dermomurex antonius</i>
Thaididae
<i>Cronia avellana</i>
Columbellidae
<i>Zafra mitriformis</i>
Fascioliidae
<i>Latirus walkeri</i>
Mitridae
<i>Mitra backae</i>
<i>M. chalybeia</i>
<i>M. gilbertsoni</i>
<i>M. hansenae</i>
<i>M. marrowi</i>
Volutidae
<i>Amoria elliotti</i>
<i>A. grayi</i>
<i>A. irvinae</i>
<i>A. macandrewi</i>
<i>A. nivosa</i>
<i>Volutoconus coniformis</i>
<i>V. hargreavesi</i>
Conidae
<i>Conus clarus</i>
<i>C. dorreensis</i>
<i>C. kenyonae</i>
<i>C. nodulosus</i>
Terebridae
<i>Duplicaria crakei</i>

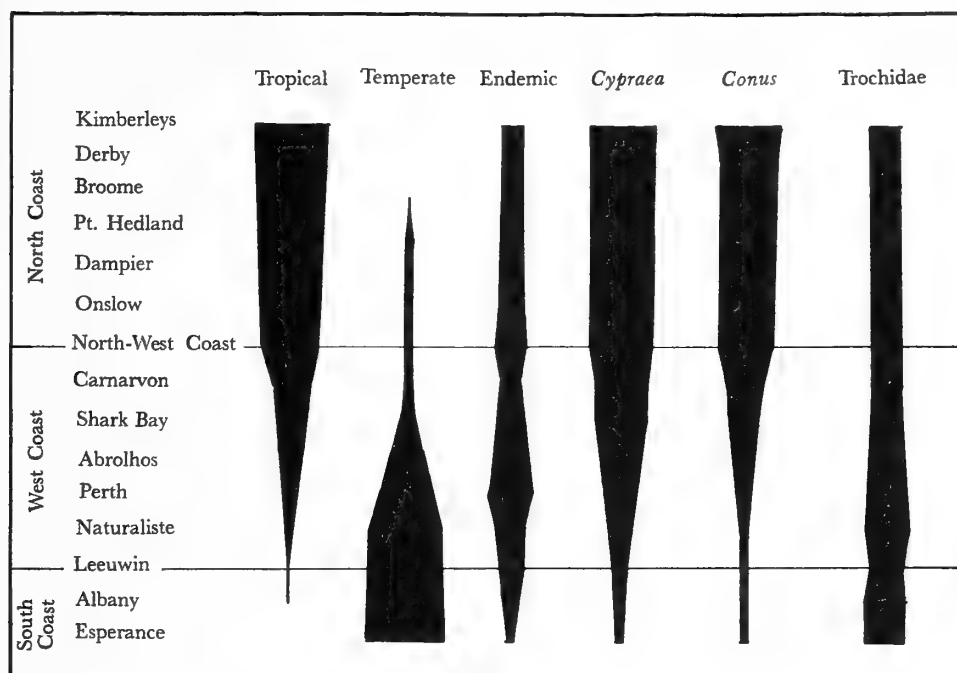


Figure 2

Distribution of marine prosobranch gastropods in Western Australia

There is a tendency for the Houtman Abrolhos and Rottnest Island to have a more tropical fauna than the adjacent inshore areas; this is particularly true of the Abrolhos. At Geraldton, 60 km east of the Abrolhos, the coastal fauna is much more temperate in nature, though the percentages of tropical species used here do not indicate this. The difference between the molluscan faunas of the Abrolhos and Geraldton could be better shown by a detailed analysis which included relative abundances instead of just presence and absence. The ocean waters at Geraldton reach a minimum of 18°C during the winter (HODGKIN & PHILLIPS, 1969), while the minimum at the Abrolhos is 19°C (MARSH, 1976). The difference, though small, is crucial since a minimum of 20°C is generally accepted as the limit of a tropical fauna (BRIGGS, 1975).

Distribution of the Family Cypraeidae

The genus *Cypraea* has been extensively studied in Western Australia. CATE (1964; 1968) and WILSON & GILLET (1971) provide data on the distributions of almost all of the cowries occurring in the State. In addition, WILSON & SUMMERS (1966) and WILSON & McCOMB (1967) discuss the systematics and distributions of the members of the subgenus *Zoila* in detail.

The genus *Cypraea* is characteristic of shallow tropical marine environments. The distribution of the 61 species recorded in Western Australia is shown on Figure 2, which clearly demonstrates the tropical nature of the group. Fifty of the species are tropical, 5 are temperate and 6 are endemic. The tropical *Cypraea* follow the generalized dis-

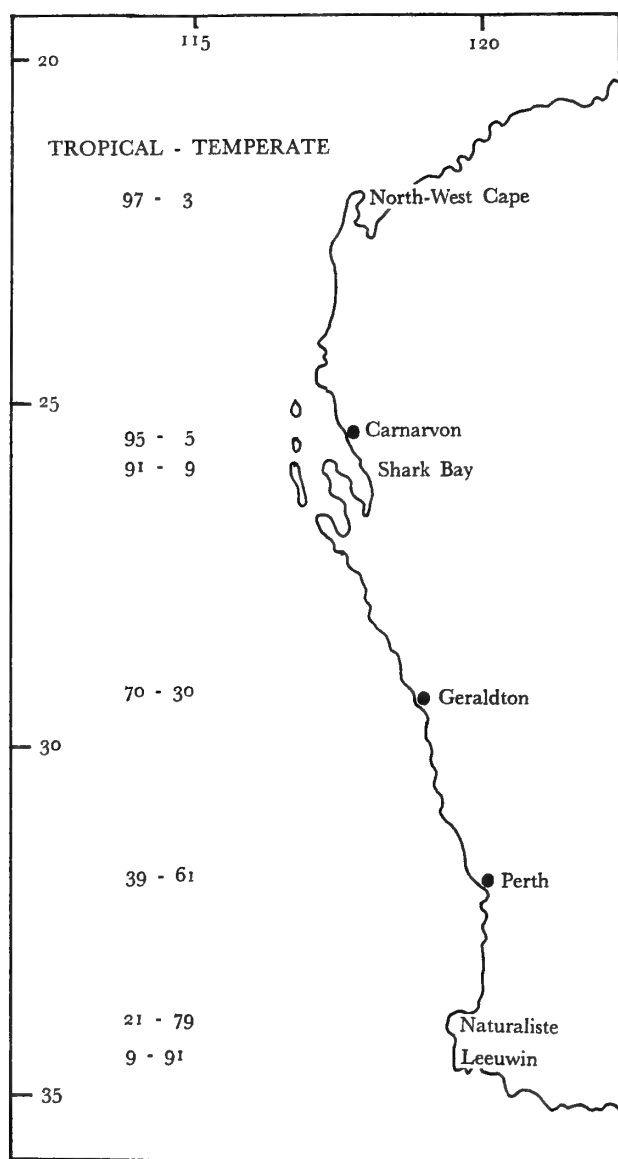


Figure 3

Percentages of tropical (left) and temperate (right) marine prosobranch species along the west coast of Western Australia. These figures exclude endemic species

tribution pattern discussed above. Nine species have been collected only along the north coast east of North-West Cape and an additional 10 have been reported at but not south of North-West Cape. The number of tropical *Cypraea* declines sharply along the west coast, and only 12

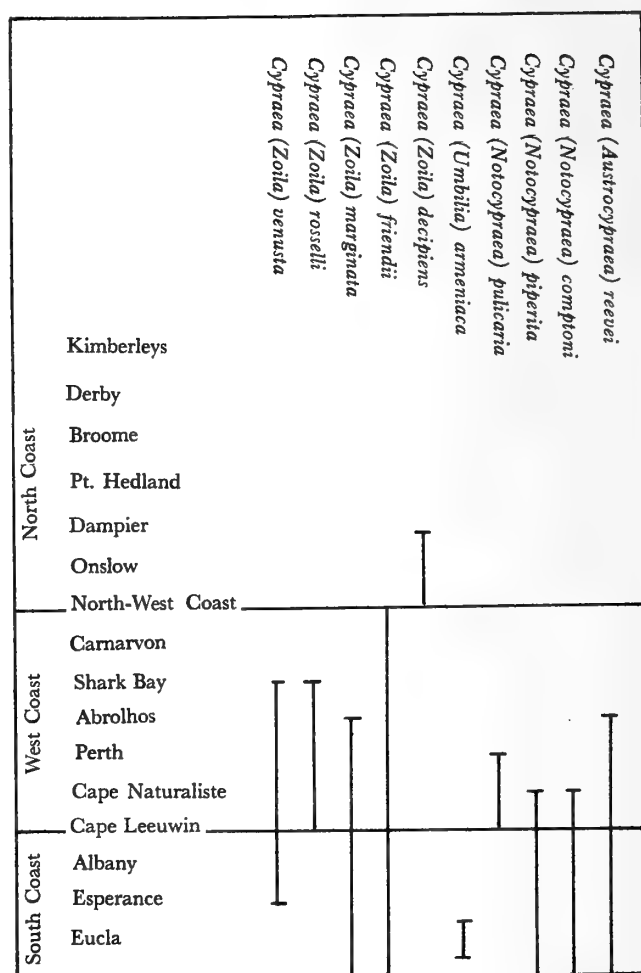


Figure 4

Distribution of cowries of the subgenera *Austrocypraea*, *Notocypraea*, *Umbilia*, and *Zoila* in Western Australia

have been reported south of the Houtman Abrolhos. South of the Abrolhos there is a gradual decline in the number of tropical species. The extreme ranges are exhibited by *C. helvola* and *C. caputserpentis*, which range along the south coast to Albany.

Four subgenera of *Cypraea*, with a total of 14 species, are restricted to Australia: *Austrocypraea*, *Notocypraea*, *Umbilia*, and *Zoila*. Nine species of these subgenera occur in Western Australia, and 5 are endemic to the State (Figure 4). Eight of the 9 species are found predominately in the coldwater areas of the lower west coast and the south

coast. Only one species, *Cypraea* (*Zoila*) *decepiens*, is found on the north coast, where it is distributed between North-West Cape and the Buccaneer Archipelago.

Aside from the members of the Australian subgenera only a single species of *Cypraea*, *C. brevidentata*, is endemic to Western Australia. This species is restricted to the north coast between North-West Cape and Broome.

Distribution of the Family Conidae

Another tropical genus, *Conus*, has 49 representatives in Western Australia. Five of these are endemic and 5 are temperate species (Figure 2). The North-West Cape area is again the major distributional limit of the tropical species, with 15 species not being recorded farther to the south. Shark Bay and the Houtman Abrolhos are the other major limits for cones, and only one tropical species, *C. lividus*, reaches as far south as Rottnest Island.

Distribution of the Family Trochidae

In contrast to the 2 families just discussed the trochids have a fairly even split of tropical (14 species) and temperate (20) forms. Three species: *Calliostoma ciliaris*, *C. lepidus* and *Clanculus occidus* are limited to Western Australia. The number of species of tropical trochids declines progressively southward along the coast (Figure 2) with no major distributional limits. The southern species show a similar pattern, with a gradual decrease in the number of species proceeding northward.

Distribution of the Family Volutidae

The highest rate of endemism occurs in the neogastropod family Volutidae, where 7 of the 23 species, or 30%, are endemic. In addition, *Amoria dampieria* is distributed primarily in Western Australia but extends into the Northern Territory. Volutes reproduce by depositing benthic egg capsules from which the young emerge as crawling juveniles (WILSON & GILLET, 1971). The lack of a pelagic distributional stage contributes substantially to the high rate of endemism in the group.

The distributions of the endemic volutes are shown on Figure 5. The figure shows that not only are these species endemic to Western Australia, but two have restricted distributions within the State. *Amoria macandrewi* is found only off Barrow Island and Monte Bello Island, a distance of only 50 km. *Amoria ellioti* has a range of 200 km from Dampier to Port Hedland. Both species are found in shal-

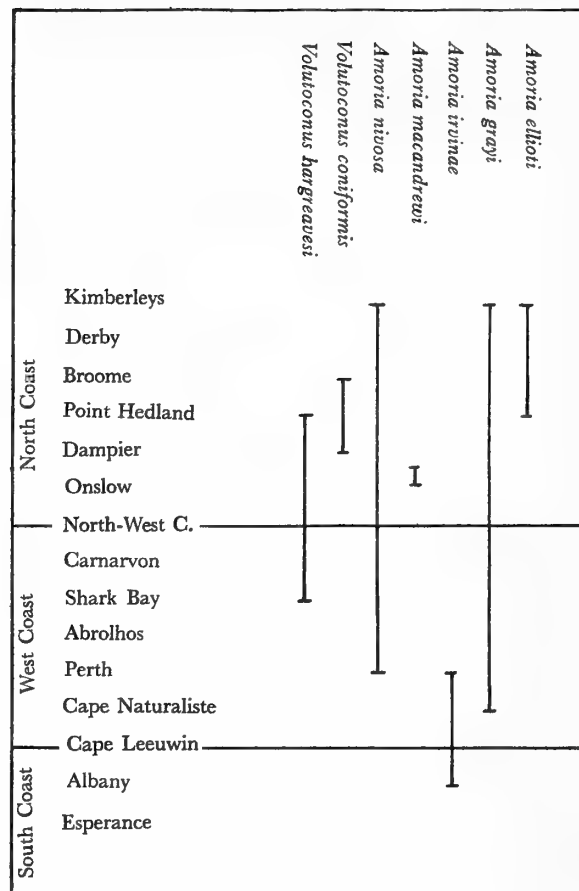


Figure 5

Distribution of volute species endemic to Western Australia

low waters and their known ranges are not likely to be extended substantially by continued collecting.

In contrast to the species with restricted ranges are several endemics found over large portions of the Western Australian coastline. *Amoria grayi* extends along the entire north coast westward from the Kimberleys and southward on the west coast to Cape Naturaliste. *Amoria irvinae* has a southern distribution from Albany on the south coast to Jurien Bay on the west coast. Three other species (*Amoria nivosa*, *Volutoconus coniformis* and *V. hargreavesi*) have distributions over reasonably wide areas of the coastline. Thus there is substantial variation in the ranges occupied by the volutes endemic to Western Australia. It would be interesting to elucidate the mechanisms which account for these variations.

DISCUSSION

The detailed analysis of prosobranch distributions along the coast of Western Australia presented here elaborates the general outlines presented by HEDLEY (1926), WILSON & GILLET (1971), and WILSON & STEVENSON (1977). There are two distinct faunas in the State: a northern tropical fauna which extends into eastern Australia and the Indo-Pacific region and a warm temperate fauna which is continuous with the remainder of the coastline of southern Australia. Most of the tropical species reach the North-West Cape area and almost all of the temperate forms are distributed along the south coast to Cape Leeuwin. The two faunas overlap on the west coast between Cape Leeuwin and North-West Cape, with the major overlap area located between Perth and the Houtman Abrolhos.

The division of the Western Australian coastline into faunal regions has received attention from a number of workers investigating different phyla. The tropical coast of Australia was divided into a Solanderian fauna east of Cape York and a Damperian fauna extending from the west of Cape York to the Houtman Abrolhos and Geraldton (HEDLEY, 1926). This pattern was followed for echinoderms by CLARK (1946) and MARSH (1976) but ENDEAN (1957) suggested merging the Damperian and Solanderian faunas into a single tropical Australian province. MARSH (*op. cit.*) rejected this proposal because 20% of the shallow-water asteroids of north Western Australia are endemic to the waters west of Torres Strait. Eighty-eight percent of the prosobranch gastropods investigated here which occur on the north coast of Western Australia also occur in eastern Queensland or the Indo-Pacific region. This suggests that in the case of prosobranchs there is no need to subdivide the tropical waters of Australia into two faunal regions, and to do so would obscure the extensive similarities between the two areas. A similar conclusion was reached by WILSON & STEVENSON (1977) in their discussion of the distributions of cardiid bivalves.

HEDLEY (1926) described an Adelaidean region, which has since been renamed the Flindersian region; extending along the south coast of Australia westward from Bass Strait, and including all of the south coast of Western Australia and the west coast to Geraldton. The Flindersian region was subsequently restricted to the south coast east of Albany by KOTT (1952) and a Baudinian region established between Perth and Albany. The proposal of a separate Baudinian region was based on four species of ascidians endemic to the area. Figure 2 shows that while a number of endemic prosobranchs occur between Albany and Perth, most extend further to the north or are found

entirely outside Kott's Baudinian region. The analysis of prosobranch distributions indicates that there is no necessity for the separation of the lower west coast into a distinct faunal area.

As has been indicated, the major overlap zone between the tropical and temperate prosobranchs occurs in the region of Perth to the Houtman Abrolhos and Geraldton. Since the marine fauna at Geraldton has a distinctly more temperate character than the offshore Abrolhos the placement of the northern limit of the Flindersian region at Geraldton by HEDLEY (1926) is substantiated.

Similarly ENDEAN (1957) divided the fauna of the Queensland coast into two groups: an inshore component influenced by freshwater runoff from adjacent land masses and an offshore reef area. A similar inshore and offshore division could be made on the Western Australian coast, but there would be a substantial overlap between the two groups.

The overall rate of endemism, 8.6%, is low. Among the species presently regarded as endemic are 9 described since 1965. The ranges of these species are poorly known and some of them may well be eventually found outside of Western Australia. Undoubtedly other new forms may be described as the molluscan fauna of Western Australia receives more attention. Some of the endemic species whose distributions are well established are clearly valid species. Included in this category are species such as *Conus dorreensis* which cannot be confused with any other species. Many of the shallow-water forms occurring along the Western Australian tropical coastline are closely related to, or conspecific with, populations in the Indo-Pacific region or eastern Australia. The populations in Western Australia have diverged from the main body of the species because of reproductive isolation, but whether they have diverged sufficiently to achieve species status is a matter of taxonomic judgement. One example of this is *Conus nodulosus* which is regarded as a species in this paper and by WILSON & GILLET (1971). However, Wilson and Gillett state that the status of the species is uncertain. It has a close affinity to *C. victoriae* and may prove on detailed investigation to be a subspecies of *C. victoriae*. The different judgements on such questions that could be made by taxonomists affect the rate of endemism presented here. The rate of 8.6% endemics is not an unchallenged figure, but it does indicate the presence in Western Australia of a low proportion of prosobranch species unique to the area.

Two factors appear to be important in limiting species in Western Australia: temperature and the availability of suitable habitats. The limiting role of temperature is well known (see BRIGGS, 1975). Temperate species en-

counter progressively warmer waters further north on the west coast until the upper tolerance limit is met; tropical species encounter colder waters to the south. The temperature tolerance range of each species is modified by a suite of physical and biological environmental factors, but at some point the limit is encountered and the species can go no further.

The Perth area is the northern limit for one-third of the temperate species. Most of these prosobranchs live on rocky substrates that are largely lacking in the area between Perth and Geraldton. It seems likely that some of these species would be able to colonize the shorelines further north if suitable substrates were available. Many of the tropical species live on coral reefs, and the absence of some of the reef habitats south of North-West Cape may limit tropical prosobranch species. This evades the question of why coral development is restricted south of North-West Cape, and the factor(s) limiting coral development may also be acting on the molluscs.

The pattern of oceanic surface currents along the faunal overlap zone of the west coast obviously has an important bearing on the distributions of marine prosobranch species, most of which have planktonic larval stages. The current structure is poorly known. A Western Australian Current flows northward offshore of the Continental Shelf during the summer months of November to March (WYRTKI, 1973). A southerly flowing countercurrent has recently been found over the shelf (STEEDMAN *et al.*, 1977). This brings warm surface waters southward along the west coast, with the 26° C isotherm reaching as far south as 31° S, just north of Perth. During the winter months the countercurrent dissipates and a series of semi-permanent vortices is established on the west coast. Surface temperatures over the Continental Shelf are 2° to 7° C higher than in the waters west of the Continental Shelf (STEEDMAN *et al.*, 1977). The relatively warm surface waters moved southward by the currents allow tropical prosobranch species to extend further to the south than would otherwise be the case.

ACKNOWLEDGMENTS

This paper is based on Western Australian Museum collections developed by two curators, Dr. B. R. Wilson and Mrs. S. M. Slack-Smith. Without their work and that of a number of specialists who have identified particular groups over the last 14 years this paper could not have been written. Drs. R. W. George and B. R. Wilson critically read the manuscript and made a number of very

helpful suggestions. Mrs. G. Hansen examined the species distributions. Mrs. M. Wallis typed this and a number of my other manuscripts.

APPENDIX

HALIOTIDAE

- Haliotis asinina* Linnaeus, 1758. North coast eastwards from North-West Cape.
H. conicopora Péron, 1816. South coast and northwards along the west coast to Fremantle.
H. cyclobates Péron, 1816. South coast westwards to Albany.
H. elegans Philippi, 1899. South coast westwards from Albany and northwards along the west coast to the Houtman Abrolhos.
H. ovina Gmelin, 1791. North coast eastwards from Barrow Island.
H. roei Gray, 1826. South coast and northwards along the west coast to Shark Bay.
H. scalaris (Leach, 1814). South coast and northwards along the west coast to Jurien Bay.
H. semiplicata Menke, 1843. South coast westwards from Esperance and northwards along the west coast to Perth.
H. squamata Reeve, 1846. North coast and southwards along the west coast to Shark Bay.
H. varia Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.

TROCHIDAE

- Angaria tyria* (Reeve, 1843). North coast and southward along the west coast to Cockburn Sound.
Austrocochlea constricta (Lamarck, 1822). South coast and northward along the west coast to the Houtman Abrolhos.
A. rudis (Gray, 1826). South coast and northward along the west coast to the Murchison River.
Calliostoma australe (Broderip, 1835). South coast and northward along the west coast to Fremantle.
C. ciliaris (Menke, 1843). South coast westward from Esperance and northwards along the west coast to Perth.
C. interruptum (Wood, 1828). South coast and northward along the west coast to Rottnest.
C. lepidus (Philippi, 1846). West coast from Jurien Bay to the Houtman Abrolhos.
C. monile (Reeve, 1843). North coast eastwards from Monte Bello Island.
C. spinulosum Tate, 1893. North coast and southward along the west coast to Rottnest Island.
Cantharidella beachportensis (Cotton and Godfrey, 1934). South coast and northward along the west coast to Cape Naturaliste.
C. ocellina (Hedley, 1911). South coast and northward along the west coast to Rottnest Island.
Clanculus atropurpureus (Gould, 1846). North coast and southward along west coast to Kalbarri.

- C. consorbrinus* Tate, 1893. North coast, west coast, and eastward on south coast to Albany.
- C. denticulatus* (Gray, 1827). South coast and northward along the west coast to the Houtman Abrolhos.
- C. dunkeri* (Koch, 1843). South coast as far west as Albany.
- C. limbatus* (Quoy and Gaimard, 1834). South coast and northward along the west coast to Bunbury.
- C. maxillatus* (Menke, 1843). South coast and northward along the west coast to Kalbarri.
- C. occiduus* Cotten & Godfrey, 1934. South coast from Hopetoun west and northward along the west coast to Rottnest Island.
- C. personatus* (Philippi, 1846). South coast and northward along the west coast to Rottnest Island.
- C. plebejus* (Philippi, 1851). South coast and northward along the west coast to Geraldton.
- C. ringens* (Menke, 1843). South coast and northward along the west coast to Perth.
- Gibbula maccullochi* Hedley, 1907. North coast and southward along the west coast to Perth.
- G. preissiana* (Philippi, 1848). South coast and northward along the west coast to Perth.
- Monilea callifera* (Lamarck, 1827). North coast and southward along the west coast to Cockburn Sound.
- Monodonta labio* (Linnaeus, 1758). North coast and southward along the west coast to Shark Bay.
- Odontotrochus* cf. *O. baudini* (Fischer, 1878). North coast and southward along the west coast to Fremantle.
- O. chlorostoma* (Menke, 1843). South coast and northward along the west coast to North-West Cape.
- Phasianotrochus eximus* (Perry, 1811). South coast and northward along the west coast to Fremantle.
- Prothalotia lehmanni* (Menke, 1843). South coast and northward along the west coast to Kalbarri.
- P. pulcherrima* (Wood, 1828). South coast and northward along the west coast to the Houtman Abrolhos.
- P. ramburi* (Crosse, 1864). South coast and northward along the west coast to Cape Naturaliste.
- Tectus pyramis* Born, 1778. North coast and southward along the west coast to Rottnest Island.
- Thalotia conica* (Gray, 1827). South coast and northward along the west coast to Rottnest Island.
- Trochus fenestratus* Tate, 1893. North coast and southward along the west coast to Shark Bay.
- T. hanleyanus* Reeve, 1842. North coast and southward along the west coast to the Houtman Abrolhos.
- T. lineatus* Lamarck, 1822. North coast eastward from North-West Cape.
- T. maculatus* Linnaeus, 1758. North coast and southward along the west coast to the Houtman Abrolhos.

TURBINIDAE

- Astraea pileola* Reeve, 1842. North coast and southward along the west coast to Carnarvon.
- A. rotularia* (Lamarck, 1822). North coast eastward from Port Hedland.
- A. squamifera* (Koch, 1844). South coast and northward along the west coast to Jurien Bay.

- A. stellare* (Gmelin, 1791). North coast eastward from North-West Cape.
- A. tentorium* (Thiele, 1931). Endemic from Cockburn Sound to the Houtman Abrolhos.
- Lunella cinereus* Born, 1798. North coast eastward from North-West Cape.
- Marmarostoma pulcher* (Reeve, 1842). South coast and northward along the west coast to Shark Bay.
- Ninella haynesi* Preston, 1914. North coast and southward along the west coast to Rottnest Island.
- N. torquata* Gmelin, 1791. South coast and northward along the west coast to Geraldton.
- Phasianella australis* (Gmelin, 1791). South coast and northward along the west coast to Geraldton.
- P. ventricosa* (Swainson, 1822). South coast and northward along the west coast to Geraldton.
- Subninelletta undulata* (Gmelin, 1791). South coast and northward along the west coast to Geraldton.
- Turbo* cf. *T. argyrostomus* Linnaeus, 1758. North coast and southward along the west coast to Carnarvon.
- T. chrysostoma* Linnaeus, 1758. North coast and southward along the west coast to Carnarvon.
- T. foliaceus* Philippi, 1846. North coast eastward from North-West Cape.
- T. jourdani* Kiener, 1839. South coast and northward along the west coast to the Houtman Abrolhos.
- T. petholatus* Linnaeus, 1758. North coast and southward along the west coast to Shark Bay.

NERITIDAE

- Nerita albicilla* Linnaeus, 1758. North coast and southward along the west coast to the Abrolhos.
- N. atramentosa* Reeve, 1855. South coast and northwards along the west coast to North-West Cape.
- N. chamaeleon* Linnaeus, 1758. North coast eastwards from North-West Cape.
- N. lineata* Gmelin, 1791. North coast and southward along the west coast to Shark Bay.
- N. plicata* Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
- N. reticulata* Karsten, 1789. Kimberley region of the north coast.
- N. undata* Linnaeus, 1758. North coast and southwards along the west coast to Shark Bay.

LITTORINIDAE

- Bembicium auratum* (Quoy and Gaimard, 1834). South coast and northward along the west coast to the Houtman Abrolhos.
- B. melanostoma* (Gmelin, 1791). South coast and northward along the west coast to Perth.
- Littorina scabra* (Linnaeus, 1758). North coast and southward along the west coast to Shark Bay.
- L. undulata* Gray, 1939. North coast eastward from North-West Cape.
- L. unifasciata* Gray, 1826. South coast and northward along the west coast to North-West Cape.

- Nodilittorina australis* (Gray, 1826). Endemic from Esperance to North-West Cape.
N. nodosa (Gray, 1839). Endemic from Geraldton to the north coast.
N. pyramidalis (Quoy and Gaimard, 1833). North coast and southward along the west coast to Fremantle.
Tectarius rusticus (Philippi, 1846). Endemic to the Kimberley region.

STROMBIDAE

- Lambis chiragra* (Linnaeus, 1758). North coast eastwards from North-West Cape.
L. lambis (Linnaeus, 1758). North coast eastwards from North-West Cape.
Strombus campbelli Griffith and Pidgeon, 1834. North coast and southwards along the west coast to Fremantle.
S. dilatatus Swainson, 1821. North coast eastwards from North-West Cape.
S. epidromus Linnaeus, 1758. North coast eastwards from North-West Cape.
S. gibberulus Linnaeus, 1758. North coast eastwards from North-West Cape.
S. lentiginosus Linnaeus, 1758. North coast eastwards from the Dampier Archipelago.
S. marginatus Duclos, 1844. North coast eastwards from North-West Cape.
S. mutabilis Swainson, 1821. North coast and southwards along the west coast to Cape Leeuwin.
S. plicatus (Röding, 1798). North coast eastwards from Onslow.
S. urceus Linnaeus, 1758. North coast eastwards from North-West Cape.
S. vomer (Röding, 1798). North coast and southwards along the west coast to Shark Bay.
S. wilsoni Abbott, 1967. North coast east from North-West Cape.
Rimella cancellata Lamarck, 1816. North coast eastwards from the North-West Cape.
Terebellum terebellum (Linnaeus, 1758). North coast eastwards from North-West Cape.

CYPRAEIDAE

- Cypraea annulus* Linnaeus, 1758. North coast southwards along the west coast to Rottnest Island.
C. arabica Linnaeus, 1758. North coast southwards along the west coast to Shark Bay.
C. argus Linnaeus, 1758. Along the north coast eastwards from North-West Cape.
C. armeniaca Verco, 1912. South coast as far westwards as Eucla.
C. asellus Linnaeus, 1758. Along the north coast eastwards from North-West Cape.
C. brevidentata Sowerby, 1870. North coast endemic between North-West Cape and Broome.
C. caputserpentis Linnaeus, 1758. North coast, southwards on the west coast, continuing on to Albany on the south coast.
C. carneola Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
C. caurica Linnaeus, 1758. North coast southwards along the west coast to Shark Bay.

- C. cernica* Sowerby, 1870. North coast and southwards along the west coast to Bunbury.
C. chinensis Lamarck, 1822. Along the north coast eastwards from North-West Cape, and southwards on the west coast to Cape Naturaliste.
C. cicercula Linnaeus, 1758. North coast eastwards from North-West Cape.
C. clandestina Linnaeus, 1767. North coast and southwards along the west coast to Cape Naturaliste.
C. comptoni Gray, 1847. South coast to Cape Naturaliste.
C. cribraria Linnaeus, 1758. North coast southwards on the west coast to Cape Naturaliste.
C. cylindrica Born, 1778. North coast southwards on the west coast to Shark Bay.
C. decipiens Smith, 1880. Along the north coast from North-West Cape to the Buccaneer Archipelago.
C. eglantina Duclos, 1833. North coast and southwards along the west coast to the Houtman Abrolhos.
C. erosa Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
C. erroneus Linnaeus, 1758. North coast and southwards along the west coast to Cape Naturaliste.
C. fimbriata Gmelin, 1791. North coast southwards along the west coast to Cape Naturaliste.
C. friendii Gray, 1831. South coast and northwards along the west coast to North-West Cape.
C. gracilis Broderip and Sowerby, 1829. North coast southwards along the west coast to Cape Naturaliste.
C. hammondae (Iredale, 1939). North coast southwards along the west coast to the Houtman Abrolhos.
C. helvola Linnaeus, 1758. North coast southwards along the west coast and along the south coast to Albany.
C. hirundo Linnaeus, 1758. North coast and southwards along the west coast to Shark Bay.
C. histrio Gmelin, 1791. Along the north coast eastwards from North-West Cape.
C. isabella Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
C. kieneri Hidalgo, 1906. North coast eastwards from North-West Cape.
C. labrolineata Gaskoin, 1848. North coast eastwards from North-west Cape.
C. limacina Lamarck, 1810. North coast and southwards along the west coast to Cape Naturaliste.
C. lutea Gmelin, 1791. North coast eastwards from North-West Cape.
C. lynx Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
C. marginata Lamarck, 1811. South coast and northwards along the west coast to Geraldton.
C. mauritania Linnaeus, 1758. North coast in the Kimberley area.
C. miliaris Gmelin, 1791. North coast and southwards along the west coast to Shark Bay.
C. moneta Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
C. nucleus Lamarck, 1811. Along the north coast eastwards from North-West Cape.
C. ovum Gmelin, 1791. North coast and southwards along the west coast to the Houtman Abrolhos.

- C. pallidula* Gaskoin, 1849. North coast and southwards along the west coast to Cape Naturaliste.
- C. piperita* Gray, 1825. South coast and northwards along the west coast to Cape Naturaliste.
- C. poraria* Linnaeus, 1758. Along the north coast and southward on the west coast to Cape Naturaliste.
- C. pyriformis* Gray, 1824. Along the Kimberley region of the north coast.
- C. pulicaria* Reeve, 1846. West coast from Cape Leeuwin to Rott-nest Island.
- C. punctata* Linnaeus, 1771. North coast eastwards from North-West Cape.
- C. quadrimaculata* Gray, 1824. Along the north coast in the Kimberley region.
- C. reevei* Sowerby, 1832. South coast northwards along the west coast to the Houtman Abrolhos.
- C. rosselli* (Cotton, 1948). West coast from Cape Leeuwin to Shark Bay.
- C. saulae* Gaskoin, 1843. Along the north coast eastwards from the Dampier Archipelago.
- C. staphylaea* Linnaeus, 1758. North coast and southwards along the west coast to Rottnest Island.
- C. stolidia* Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
- C. subviridis* Reeve, 1835. North coast and southwards along the west coast to Rottnest Island.
- C. talpa* Linnaeus, 1758. Along the north coast eastwards from North-West Cape.
- C. teres* Gmelin, 1791. North coast and southwards along the west coast to Cape Naturaliste.
- C. testudinaria* Linnaeus, 1758. Along the Kimberley region of the north coast.
- C. tigris* Linnaeus, 1758. North coast and southwards along the west coast to the Houtman Abrolhos.
- C. ursellus* Gmelin, 1791. Along the north coast eastwards from Broome.
- C. venusta* Sowerby, 1847. South coast northwards along the west coast to Shark Bay.
- C. vitellus* Linnaeus, 1758. North coast and southwards along the west coast to Cape Naturaliste.
- C. walkeri* Sowerby, 1832. Along the north coast eastwards from Broome.
- C. ziczac* Linnaeus, 1758. North coast and southwards along the west coast to Shark Bay.

NATICIDAE

- Ectosinum zonale* (Quoy and Gaimard, 1833). South coast and northward along the west coast to Rottnest Island.
- Eunaticina dingeldi* (Iredale, 1931). South coast, west along the coast, and eastward along the north coast to Broome.
- Mammilla opaca* (Récluz, 1851). North coast and southward along the west coast to Shark Bay.
- M. simiae* (Deshayes, 1838). North coast eastward from the Dampier Archipelago.
- Mamillaria powisiana* (Récluz, 1844). North coast and southward along the west coast to Geraldton.

- Natica fasciata* (Röding, 1798). North coast eastward from the Dampier Archipelago.
- N. gualtieriana* Récluz, 1844. North coast, west coast, and eastward along the south coast to Albany.
- N. sagittata* Menke, 1843. North coast, west coast, and eastward along the south coast to Esperance.
- N. seychellium* Watson, 1886. North coast and southward along the west coast to Cape Naturaliste.
- Sigaretotrema umbilicatum* (Quay and Gaimard, 1833). South coast and northward along the west coast to Perth.

CASSIDAE

- Casmaria erinacea* (Linnaeus, 1758). North coast eastward from North-West Cape.
- C. ponderosa* (Gmelin, 1791). North coast eastward from Barrow Island.
- Cassis cornuta* (Linnaeus, 1758). North coast eastward from Onslow.
- C. fimbriata* Quoy and Gaimard, 1833. South coast and northward along the west coast to the Houtman Abrolhos.
- Phalium adcocki* (Sowerby, 1896). South coast as far westward as Eucla.
- P. areola* (Linnaeus, 1758). North coast and southward along the west coast to Carnarvon.
- P. bandatum* (Perry, 1811). North coast and southward along the west coast to the Houtman Abrolhos.
- P. bisulcatum* (Schubert and Wagner, 1829). North coast and southward along the west coast to Carnarvon.
- P. glabratum* (Iredale, 1927). Kimberley region of the north coast.
- P. pauciruge* (Menke, 1843). South coast as far northward as Shark Bay.
- P. pyrum* (Lamarck, 1822). South coast as far westward as Bremer Bay.
- P. semigranosum* (Lamarck, 1822). South coast and northward along the west coast to Fremantle.
- P. sinuosum* (Verco, 1904). South coast and northward along the west coast to Bunbury.
- P. whitworthi* Abbott, 1968. West coast from Rottnest to Geraldton.

TONNIDAE

- Tonna allium* (Dillwyn, 1817). North coast eastward from North-West Cape.
- T. canaliculata* (Linnaeus, 1758). North coast and southward along the west coast to Shark Bay.
- T. chinensis* (Dillwyn, 1817). North coast and southward along the west coast to Cape Leeuwin.
- T. perdix* (Linnaeus, 1758). North coast and southward along the west coast to the Houtman Abrolhos.
- T. tessellata* (Linnaeus, 1758). North coast eastward from the Dampier Archipelago.
- T. variegata* (Lamarck, 1822). South coast and northward along the west coast to North-West Cape.

MURICIDAE

- Bedeve hanleyi* (Angas, 1867). South coast and northward along the west coast to Shark Bay.
- B. paivae* (Crosse, 1864). South coast and northward along the west coast to Pt. Quobba.
- Chicoreus banksii* (Sowerby, 1840). North coast eastward from the Dampier Archipelago.
- C. cervicornis* (Lamarck, 1822). North coast and southward along the west coast to Rottnest Island.
- C. cornucervi* (Röding, 1798). North coast and southward along the west coast to the Houtman Abrolhos.
- C. laciniatus* (Sowerby, 1841). North coast eastward from Onslow.
- C. ramosus* (Linnaeus, 1758). Kimberley region of the north coast.
- C. rubiginosus* (Reeve, 1845). North coast and southward along the west coast to the Houtman Abrolhos.
- C. torrefactus* (Sowerby, 1841). North coast eastward from North-West Cape.
- Dermomurex antonius* Vokes, 1974. Dampier Archipelago area of the north coast.
- Haustellum macgillivrayi* (Dohrn, 1862). North coast eastward from North-West Cape and southwards on the west coast to Jurien Bay.
- H. multiplicatum* (Sowerby, 1895). North coast and southward along the west coast to Rottnest Island.
- H. wilsoni* Old and d'Attilio, 1971. West coast in the Jurien Bay area.
- Hexaplex stainforthi* (Reeve, 1842). North coast and southward along the west coast to the Houtman Abrolhos.
- Homalocantha secunda* (Lamarck, 1822). North coast eastward from North-West Cape.
- Murex acanthostephes* Watson, 1883. North coast eastward from Broome.
- M. brunneus* (Link, 1807). Kimberley region of the north coast.
- M. coppingeri* E. A. Smith, 1884. North coast eastward from North-West Cape.
- M. triremus* (Perry, 1811). North coast and southward along the west coast to Shark Bay.
- Muricopsis planilirata* (Reeve, 1845). South coast and northward along the west coast to Perth.
- Pterotyphis angasi* (Crosse, 1863). South coast and northward along the west coast to Fremantle.
- Pterynotus acanthopterus* (Lamarck, 1816). North coast and southward along the west coast to Cape Leeuwin.
- P. bednalli* (Brazier, 1877). Kimberley region of the north coast.
- P. lowei* (Pilsbry, 1931). North coast eastward from the Dampier Archipelago.
- P. westralis* Ponder and Wilson, 1973. West coast from Bunbury to North-West Cape.
- Typhis yatesi* Crosse and Fischer, 1865. South coast and northward along the west coast to Rottnest Island.

THAIDIDAE

- Cronia avellana* (Reeve, 1846). North coast, west coast, and eastwards along the south coast to Albany.
- Dicathais aegrola* (Reeve, 1846). South coast and northward along the west coast to the Houtman Abrolhos.

- Drupa morum* Röding, 1798. North coast eastwards from North-West Cape.
- D. ricinus* (Linnaeus, 1758). North coast and southward along the west coast to the Houtman Abrolhos.
- Drupella cornus* (Röding, 1798). North coast and southwards along the west coast to the Houtman Abrolhos.
- Drupina grossularia* Röding, 1798. North coast eastwards from Barrow Island.
- D. lobata* (Blainville, 1832). North coast eastwards from North-West Cape.
- Lepsiella flindersi* Adams and Angas, 1863. South coast and northwards along the west coast to Cockburn Sound.
- L. vinosa* (Lamarck, 1822). South coast and northwards along the west coast to Cockburn Sound.
- Manicella manicella* (Linnaeus, 1758). North coast and southwards along the west coast to Shark Bay.
- M. tuberosa* (Röding, 1798). Kimberley region of the north coast.
- Morula granulata* (Duclos, 1832). North coast and southward along the west coast to Pt. Quobba.
- M. margariticola* (Broderip, 1832). North coast eastwards from North-West Cape.
- M. spinosa* (H. and A. Adams, 1853). North coast and southwards along the west coast to the Houtman Abrolhos.
- M. uva* (Röding, 1798). North coast and southward along the west coast to the Houtman Abrolhos.
- Nassa francolina* (Bruguière, 1789). North coast and southwards along the west coast to Rottnest Island.
- Thais aculeata* Deshayes, 1844. North coast eastwards from North-West Cape.
- T. alvina* (Röding, 1798). North coast eastward from the Dampier Archipelago.
- T. bufo* (Lamarck, 1822). North coast eastwards from North-West Cape.
- T. echinata* (Blainville, 1832). North coast and southward along the west coast to Shark Bay.
- T. kieneri* (Deshayes, 1844). North coast eastwards from North-West Cape.
- Vexilla vexillum* (Gmelin, 1791). North coast eastwards from North-West Cape.

COLUMBELLIDAE

- Dentimitrella austrina* (Gaskoin, 1852). South coast and northward along the west coast to Kalbarri.
- D. lincolniensis* (Reeve, 1859). South coast and northward along the west coast to Rottnest Island.
- D. pulla* (Gaskoin, 1852). South coast as far westward as Pt. d'Entrecasteaux.
- D. semiconvexa* (Lamarck, 1822). South coast and northward along the west coast to Cape Naturaliste.
- Lavesopus essingtonensis* (Reeve, 1859). North coast eastward from Pt. Hedland.
- Macrozafra angasi* Brazier, 1871. South coast as far westward as Hopetoun.
- M. speciosa* (Angas, 1877). South coast and northward on the west coast to Fremantle.

- Mitrella albina* (Kiener, 1841). North coast and west coast as far southward as Perth.
- M. ligula* (Duclos, 1840). North coast and west coast as far southward as Shark Bay.
- M. marquesa* (Gaskoin, 1852). North coast eastward from North-West Cape.
- M. miser* (Sowerby, 1844). North coast and southward along the west coast to Pt. Quobba.
- M. puella* (Sowerby, 1844). North coast eastward from North-West Cape.
- Pseudamyoia dermestoides* (Lamarck, 1822). South coast and northward along the west coast to Cape Naturaliste.
- Pyrene bidentata* (Dall, 1889). South coast and northward along the west coast to North-West Cape.
- P. flava* (Bruguière, 1789). North coast eastwards from North-West Cape.
- P. punctata* (Bruguière, 1789). North coast and southward along the west coast to the Houtman Abrolhos.
- P. testudinaria* (Link, 1807). North coast eastward from the North-West Cape.
- P. tuturina* (Lamarck, 1822). North coast and southward along the west coast to the Houtman Abrolhos.
- P. varians* (Sowerby, 1832). North coast and southward along the west coast to Rottnest Island.
- Retizafra calva* (Verco, 1910). South coast and northward along the west coast to Rottnest Island.
- Zafra mitriformis* A. Adams, 1860. Swan estuary only.
- Z. troglodytes* (Souverbie, 1866). Dampier Archipelago area of the north coast.

FASCIOLARIIDAE

- Fusinus australis* (Quoy and Gaimard, 1833). South coast and northwards along the west coast to the Houtman Abrolhos.
- F. tessellatus* (Sowerby, 1880). South coast and northwards along the west coast to Geraldton.
- Fusus colus* (Linnaeus, 1758). North coast and southwards along the west coast to Shark Bay.
- Latirus belcheri* (Reeve, 1847). North coast eastwards from North-West Cape.
- L. paetelianus* Kobelt, 1876. North coast eastwards from Onslow.
- L. recurvirostris* Schubert and Wagner, 1829. North coast eastwards from North-West Cape.
- L. walkeri* Melville, 1895. North coast eastwards from North-West Cape.
- Latirolagena smaragdula* (Linnaeus, 1758). North coast eastwards from Rowley Shoals.
- Microcolus dunkeri* (Jonas, 1844). South coast and northwards along the west coast to the Houtman Abrolhos.
- Peristernia incarnata* (Deshayes, 1830). North coast and southwards along the west coast to Geraldton.
- Pleuroploca australasia* (Perry, 1811). South coast.
- P. filamentosa* (Röding, 1798). Kimberley region of the north coast.
- P. trapezium* (Linnaeus, 1758). North coast eastwards from the Montebello Islands.

NASSARIIDAE

- Nassarius albescent* (Dunker, 1846). North coast eastwards from North-West Cape.
- N. albina* (Thiele, 1930). North coast and southward along the west coast to the Houtman Abrolhos.
- N. bicallosus* (E. A. Smith, 1876). North coast and southwards along the west coast to Shark Bay.
- N. burchari* (Dunker in Philippi, 1849). South coast and northwards along the west coast to Perth.
- N. concinnus* (Powys, 1835). North coast eastwards from North-West Cape.
- N. coronatus* (Bruguière, 1789). North coast eastwards from North-West Cape.
- N. crematus* (Hinds, 1844). Kimberley region of the north coast.
- N. dorsatus* (Röding, 1798). North coast eastwards from North-West Cape.
- N. gaudiosus* (Hinds, 1844). North coast and southwards along the west coast to Perth.
- N. glans* (Linnaeus, 1758). North coast and southwards along the west coast to Geraldton.
- N. livescens* (Philippi, 1849). North coast and southwards along the west coast to Shark Bay.
- N. nigellus* (Reeve, 1864). South coast and northwards along the west coast to Cockburn Sound.
- N. particeps* (Hedley, 1915). South coast, west coast, and north coast east to Dampier.
- N. pauperatus* (Lamarck, 1822). South coast and northwards along the west coast to Geraldton.
- N. pyrrhus* (Menke, 1843). South coast and northwards along the west coast to Fremantle.
- N. rufula* (Kiener, 1834). South coast westwards from Albany and northwards along the west coast to Geraldton.
- N. stigmarius* (A. Adams, 1852). North coast eastwards from North-West Cape.
- N. variegatus* (A. Adams, 1852). North coast eastwards from Onslow.

OLIVIDAE

- Allocochira monilifera* (Reeve, 1864). South coast and northward along the west coast to Cape Leeuwin.
- Amalda elongata* (Gray, 1847). North coast and southward along the west coast to Shark Bay.
- Ancillista cingulata* (Sowerby, 1830). North coast and southward along the west coast to Shark Bay.
- Oliva australis* Duclos, 1835. South coast, west coast, and eastward along the north coast to Broome.
- O. caerulea* (Röding, 1798). North coast and southward along the west coast to the Houtman Abrolhos.
- O. caldania* Duclos, 1835. North coast eastward from North-West Cape.
- O. lignara* Marratt, 1868. North coast and southward along the west coast to Cockburn Sound.

O. oliva (Linnaeus, 1758). North coast eastward from North-West Cape.

O. sidelia Duclos, 1835. North coast eastward from Onslow.

MITRIDAE

Cancilla circula (Kiener, 1838). North coast eastward from Onslow.

Imbricaria cf. *I. conovula* Quoy & Gaimard, 1833. North coast eastward from Dampier.

Mitra ambigua Swainson, 1829. North coast eastward from North-West Cape.

M. atjehensis Oostingh, 1939. North coast and southward along the west coast to Dongara.

M. aurantia (Gmelin, 1791). North coast eastward from Barrow Island.

M. carbonaria Swainson, 1822. South coast and northward along the west coast to the Houtman Abrolhos.

M. chalybeia Reeve, 1844. West coast endemic from Pt. d'Entrecasteaux to Port Gregory.

M. coffea Schubert and Wagner, 1829. North coast eastward from the Dampier Archipelago.

M. cucumerina Lamarck, 1811. North coast eastward from North-West Cape.

M. ferruginea Lamarck, 1811. North coast eastward from North-West Cape.

M. fraga Quoy and Gaimard, 1833. North coast and southward along the west coast to Geraldton.

M. gilbertsoni (J. Cate, 1968). Endemic from the Houtman Abrolhos to Port Hedland.

M. glabra Swainson, 1821. South coast and northward along the west coast to Perth.

M. litterata Lamarck, 1811. North coast eastward from North-west Cape.

M. luctuosa A. Adams, 1853. North coast and southward along the west coast to Perth.

M. punctulata Lamarck, 1811. North coast eastward from North-west Cape.

M. rosacea Reeve, 1845. North coast and southward along the west coast to Rottnest Island.

M. rubiginosa Reeve, 1844. North coast eastward from North-West Cape.

M. scutulata (Gmelin, 1791). North coast and southward along the west coast to Cape Naturaliste.

M. sowerbyi kingae Cernohorsky, 1972. North coast and southward along the west coast to the Houtman Abrolhos.

M. stictica (Link, 1807). Kimberley region of the north coast.

M. ticaonica Reeve, 1844. North coast and southward along the west coast to Geraldton.

M. variabilis Reeve, 1844. Eastward along the north coast from North-West Cape.

Scabricola backae Cernohorsky, 1973. Entire west coast, eastward along the north coast to Onslow.

S. desetangii (Kiener, 1838). North coast eastward from the Dampier Archipelago.

S. flammigera (Reeve, 1844). North coast eastward from Onslow.

S. incarnata (Reeve, 1845). North coast eastward from Onslow.

S. interlirata (Reeve, 1844). North coast eastward from North-West Cape.

S. lacunosa (Reeve, 1844). North coast eastward from the North-West Cape.

S. ocellata ekeræ Cernohorsky, 1973. North coast eastward from North-West Cape.

S. praestantissima Röding, 1798. North coast eastward from North-West Cape.

Vexillum amanda (Reeve, 1845). North coast and southward along the west coast to Rottnest Island.

V. angustissimum (E. A. Smith, 1903). North coast eastward from the Dampier Archipelago.

V. australe Swainson, 1820. South coast and northward along the west coast to Shark Bay.

V. cadaverosum (Reeve, 1844). North coast and southward along the west coast to Shark Bay.

V. crocatum (Lamarck, 1811). North coast eastward from the Dampier Archipelago.

V. hansenæ Cernohorsky, 1973. Endemic from Cape Leeuwin to Fremantle.

V. lincolniensis Angas, 1878. South coast as far west as Hopetoun.

V. marrowi Cernohorsky, 1973. Endemic from Hopetoun to Kalbarri.

V. microzonias (Lamarck, 1811). North coast eastward from Barrow Island.

V. modestum (Reeve, 1845). North coast eastward from Onslow.

V. obeliscus (Reeve, 1844). North coast and southward along the west coast to Rottnest Island.

V. pacificum (Reeve, 1845). North coast and southward along the west coast to Shark Bay.

V. percnodictya (Melvill, 1888). North coast eastward from North-West Cape.

V. plicarium (Linnaeus, 1758). North coast eastward from North-West Cape.

V. radius (Reeve, 1845). North coast eastward from North-West Cape.

V. rugosum (Gmelin, 1791). North coast eastward from North-West Cape.

V. suluense (Adams and Reeve, 1850). North coast eastward from North-West Cape.

V. unifasciatum (Wood, 1828). North coast and southward along the west coast to Shark Bay.

V. vulpecula (Linnaeus, 1758). North coast eastward from North-West Cape.

V. zebuense (Reeve, 1844). North coast and southward along the west coast to the Houtman Abrolhos.

VOLUTIDAE

Amoria damoni Gray, 1864. North coast and southward along the west coast to Rottnest Island.

A. dampiera Weaver, 1960. North coast eastwards from the Monte Bello Islands.

A. elliotti (Sowerby, 1864). North coast eastwards from Port Hedland.

A. exoptanda (Reeve, 1849). South coast.

A. grayi Ludbrook, 1953. North coast from the Kimberleys westward and southward along the west coast to Geographe Bay.

- A. irvinae* Smith, 1909. South coast westward from Albany and northwards along the west coast to the Houtman Abrolhos.
- A. jamrachi* Gray, 1864. North coast eastward from North-West Cape to the Kimberleys, and also occurs in Indonesia.
- A. macandrewi* (Sowerby, 1887). Region of Barrow Island.
- A. nivosa* (Lamarck, 1804). North coast and southward along the west Coast to Cockburn Sound.
- A. praetexta* (Reeve, 1849). North coast between North-West Cape and Broome.
- A. turneri* (Gray in Griffith and Pidgeon, 1834). Kimberley region of the north coast.
- Cottonia nodiplicata* (Cox, 1916). South coast and northward along the west coast to Jurien Bay.
- Ericusa fulgetrum* (Sowerby, 1825). South coast to Albany.
- E. papillosa* (Swainson, 1822). South coast and northward along the west coast to Bunbury.
- Livonia roadnightiae* (McCoy, 1881). South coast and northward along the west coast to Rottnest Island.
- Lyria mitraeformis* (Lamarck, 1811). South coast westward to Hopetoun.
- Melo amphora* (Solander, 1786). North coast and southward along the west coast to Shark Bay.
- M. miltonis* (Gray in Griffith and Pidgeon, 1834). South coast and northward along the west coast to the Houtman Abrolhos.
- Notopeplum kreuslerae* (Angas, 1865). South coast.
- Volutoconus bednalli* (Brazier, 1879). Kimberley region of the north coast.
- V. coniformis* (Cox, 1871). North coast between the Dampier Archipelago and Broome.
- V. hargreavesi* (Angas, 1872). Between Shark Bay and the Dampier Archipelago.
- CONIDAE**
- Conus achatinus* Gmelin, 1791. North coast and southward along the west coast to Jurien Bay.
- C. anemone* Lamarck, 1810. South coast and northward along the west coast to the Abrolhos Islands.
- C. arenatus* Hwass, 1792. North coast eastward from North-West Cape.
- C. capitaneus* Linnaeus, 1758. North coast eastward from North-West Cape.
- C. catus* Hwass, 1792. Kimberley region of the north coast.
- C. ceylanensis* Bruguière, 1792. North coast and southward along the west coast to Shark Bay.
- C. chaldeus* (Röding, 1798). North coast and southward along the west coast to the Houtman Abrolhos.
- C. cholmondelyi* Melvill, 1900. Kimberley region of the north coast.
- C. clarus* Smith, 1881. North coast eastward from North-West Cape.
- C. coceus* Reeve, 1844. South coast and northward on the west coast to Rottnest Island.
- C. coronatus* Gmelin, 1791. Eastward along the north coast from North-West Cape.
- C. dorreensis* Péron, 1807. South coast westward from Albany and northward on the west coast to the North-West Cape.
- C. ebraeus* Linnaeus, 1758. North coast and southward along the west coast to the Houtman Abrolhos.
- C. eburneus* Hwass, 1792. North coast eastward from Rowley Shoals.
- C. frigidus* Reeve, 1848. North coast eastwards from Barrow Island.
- C. generalis* Linnaeus, 1767. North coast eastward from North-West Cape.
- C. geographus* Linnaeus, 1758. North coast and southward along the west coast to the Houtman Abrolhos.
- C. gilvus* Reeve, 1849. North coast eastward from the Dampier Archipelago.
- C. glans* Hwass, 1792. North coast eastward from N.W. Cape.
- C. infrenatus* Reeve, 1848. West coast from Cape Naturaliste to the Houtman Abrolhos.
- C. kenyonae* Brazier, 1896. North coast and southward along the west coast to the Houtman Abrolhos.
- C. klemae* (Cotton, 1953). South coast and northwards along the west coast to the Houtman Abrolhos.
- C. lemniscatus* Reeve, 1849. North coast eastward from Adele Island.
- C. lividus* Hwass, 1792. North coast and southward along the west coast to Rottnest Island.
- C. macarae* Bernardi, 1857. North coast and southward along the west coast to Shark Bay.
- C. marmoreus* Linnaeus, 1758. North coast eastward from Rowley Shoals.
- C. miliaris* Bruguière, 1792. North coast eastward from North-West Cape.
- C. monachus* Linnaeus, 1758. North coast and southward along the west coast to Jurien Bay.
- C. mustelinus* Bruguière, 1792. Kimberley region of the north coast.
- C. nanus* Sowerby, 1833. North coast and southward along the west coast to Shark Bay.
- C. nodulosus* Sowerby, 1864. West coast from Fremantle to Shark Bay.
- C. nussatella* Linnaeus, 1758. Kimberley region of the north coast.
- C. obscurus* Sowerby, 1833. North coast eastwards from N.W. Cape.
- C. planorbis* Born, 1778. North coast eastwards from North-West Cape.
- C. pulicarius* Hwass, 1792. North coast eastward from North-West Cape.
- C. rattus* Hwass, 1792. North coast eastward from North-West Cape.
- C. rutilus* Menke, 1843. South coast and along the west coast to Rottnest Island.
- C. segravei* Gatliff, 1891. South coast westward to Cape Leeuwin.
- C. spectrum* Linnaeus, 1758. North coast and southward along the west coast to Shark Bay.
- C. sponsalis* Hwass, 1792. North coast eastward from Onslow.
- C. striatus* Linnaeus, 1758. North coast eastward from North-West Cape.
- C. suturalis* Reeve, 1844. North coast and southwards along the west coast to Shark Bay.
- C. terebra* Born, 1780. North coast and southward along the west coast to Carnarvon.
- C. tessellata* Born, 1778. Kimberley region of the north coast.

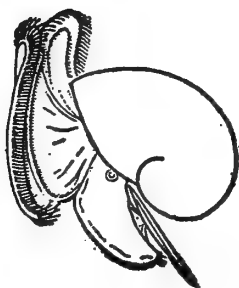
- C. textile* Linnaeus, 1758. North coast eastward from North-West Cape.
C. trigonis Reeve, 1848. North coast eastward from North-West Cape.
C. vexillum Gmelin, 1791. North coast eastward from North-West Cape.
C. victoriae Reeve, 1843. North coast eastward from North-West Cape.

TEREBRIDAE

- Duplicaria addita* Deshayes, 1859. North coast and southward along the west coast to Cape Naturaliste.
D. bernardi (Deshayes, 1857). North eastward from Broome.
D. crakei Burch, 1965. Broome area on north coast.
D. duplicata (Linnaeus, 1758). North coast and southwards along the west coast to Shark Bay.
D. evoluta (Deshayes, 1859). North coast and southward along the west coast to Shark Bay.
Hastula nitida (Hinds, 1844). North coast and southwards along the west coast to Rottnest Island.
H. rufopunctata (E. A. Smith, 1877). North coast and southward along the west coast to Shark Bay.
H. strigilata (Linnaeus, 1758). North coast eastward from Pt. Samson.
Terebra affinis Gray, 1834. North coast and southward along the west coast to the Houtman Abrolhos.
T. areolata (Link, 1807). North coast eastward from North-West Cape.
T. commaculata (Gmelin, 1791). North coast and southward along the west coast to Shark Bay.
T. crenulata (Linnaeus, 1758). North coast eastward from North-West Cape.
T. dimidiata (Linnaeus, 1758). North coast eastward from North-West Cape.
T. felina (Dillwyn, 1817). North coast eastwards from North-West Cape.
T. nebulosa Sowerby, 1825. North coast and southward along the west coast to Shark Bay.
T. triseriata Gray, 1834. North coast eastwards from Onslow.

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Predator Boreholes in *Periploma margaritaceum*, With a Brief Survey of Other Periplomatidae

(Bivalvia : Anomalodesmata)

BY

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(1 Plate; 1 Text figure)

STUDY OF THE NATIONAL MUSEUM OF NATURAL HISTORY collection of Periplomatidae revealed a population sample of *Periploma margaritaceum* (Lamarck, 1801) in which approximately 42% of the 443 valves were bored by a gastropod predator. The distribution of the boreholes appears to be fairly consistent within *P. margaritaceum*. A survey of boreholes in seven different species in the family reveals a fairly similar distribution in all specimens examined.

Predation, while long recognized as an important factor in guiding evolution, has recently received some intensive study as it affects marine animals and especially mollusks (VERMEIJ, 1978). Of the several methods of predation reviewed by Vermeij, including crushing and prying-apart of valves, swallowing whole and partial mutilation by fishes, birds, and other invertebrates, one of the most important causes of mortality is through drilling. Bivalves offer few defenses to predation other than thickened shells and some sculptural adaptations. In groups where these structural safeguards are absent, Vermeij suggests that some bivalves survive as species only by high reproductive rates.

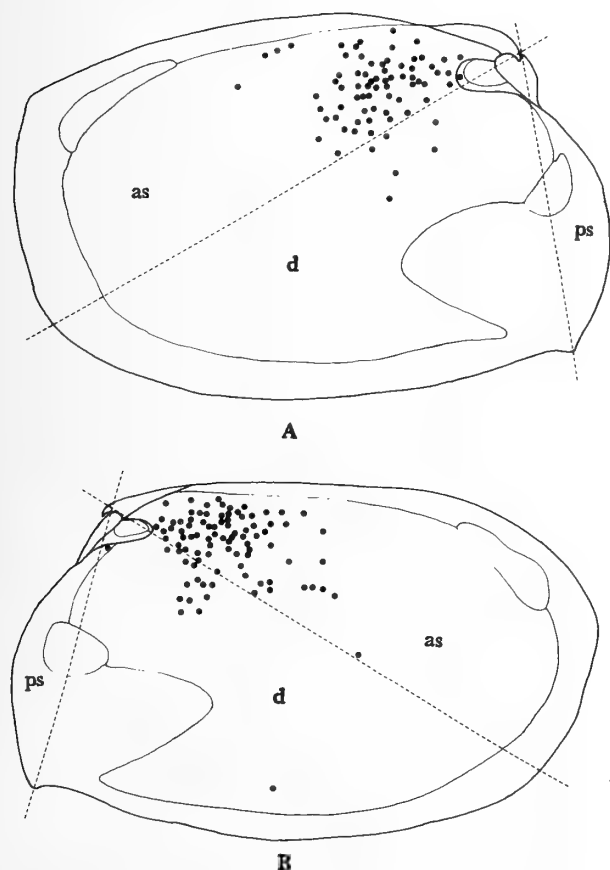
The Periplomatidae may be classed with the latter group which also includes some Tellinacea, Maत्रacea, other Pandoracea and Poromyacea, among others. Little is known of the natural history of Periplomatidae other than notes supplied by Morse (1919) for *Anatina papyracea* Say [sic, probably = *Periploma fragile* (Totten, 1835)], and the detailed study by ALLEN (1958) on *Cochlo-desma praetenue* (Pulteney, 1799). Allen's work gives the only insight we have into the habit of the family. He found *C. praetenue* to live infaunally more often on its left side in fine gravelly to muddy sand below low water

mark. Allen placed *Cochlo-desma* in Laternulidae, although it usually is considered to belong in Periplomatidae. The two families are fairly similar in many features, especially in the possession of thin shells which are split near the umbos by "transverse external slits" (MORTON, 1976). Morton suggested that some Laternulidae may protect themselves from predation with the aid of pallial eyes enabling the bivalves to initiate camouflage activities to evade predators. It is improbable that shell boring gastropods would find such defenses a deterrent to predation. Nevertheless, I was unable to find a single Laternulid shell in the collection of the U.S. National Museum of Natural History that showed evidence of having been bored. The resulting supposition could be that their defenses are most effective, but the possibility is that their partially gaping valves allow easy access to predators without the need for boring.

STANLEY (1970: 77-80) pointed out that a number of Pandoracea, the superfamily containing Periplomatidae, and members of the Tellinacea having inequivalve shells often lie on their sides within the substrate, or at least often exhibit non-vertical orientations. As Periplomatidae are uniformly inequivalve it should probably be expected that *Periploma margaritaceum* would orient itself on one side with either the right or left valve uppermost (see ALLEN, 1958). Periplomatidae probably can close their valves quite tightly utilizing the peculiar structural slit arrangement described by MORTON (1976) which allows the shells of Laternulids to function as if they consisted of four valves instead of two. It is therefore apparently necessary for a predator either to pull the valves apart, crush them or penetrate them by boring to obtain a meal. The subjects of the present study succumbed to boring.

The lot of *P. margaritaceum* alluded to above (USNM 465183/465234) contains 443 separated, recently dead valves from Matagorda Bay, Indianola, Calhoun County, Texas, collected during the early years of this century. The numbers of specimens bored and unbored are given in Table 1 and the locations of the boreholes as found in right or left valves are indicated in Table 1 and Figure 1.

The boreholes appear to be the result of predation by a gastropod, probably *Polinices duplicatus* (Say, 1822), the main naticid predator in the vicinity of Matagorda Bay (Dr. H. Harry, personal communication). They resemble those illustrated by Carriker and Yochelson (1968, pl. 2, figs. 6-9; pl. 3, figs. 2-8) which they termed "parabolic countersunk holes" (see Figure 2, herein).



Periploma margaritaceum from Matagorda Bay, Texas

Composites of 185 valves showing locations of boreholes.

A - right valve; B - left valve; dashed lines indicate areas of shells (as - anterior slope; d - disc; ps - posterior slope)

Note: due to crowding in some areas not all boreholes are indicated (see Table 1)

Table 1

Predation in *Periploma margaritaceum* from Matagorda Bay, Texas (see Figure 1)

	Number unbored	Number bored	Position of Bore Hole	
			Disc	Anterior slope
Right valve	137	83	38	45
Left valve	121	102	26	76

Some attempts have been made toward numerical localization of boreholes in gastropods (BERG & NISHENKO, 1975). In both Gastropoda and Bivalvia diagrammatic localization of holes may also be effective (ANSELL, 1960; MENGE, 1974) and has been adopted here (Figure 1). The terms anterior slope, posterior slope and disc, although not consistently applicable to all bivalve shells, are used here as follows: anterior slope = area anterodorsal to a line drawn from umbo to junction of anterior and ventral margins; posterior slope = area posterodorsal to a line drawn from umbo to junction of posterior and ventral margins; disc = the remaining central area of the shell between those lines (see Figure 1).

It should be reemphasized that right and left valves had been separated in this lot so there is little possibility for identifying complete individuals. It is assumed that the presence of a borehole in one valve of a bivalve indicates the individual was killed by this attack, and that somewhere there exists (or existed) an opposite unbored valve (see THOMAS, 1976). If we assume that this sample represents a natural assemblage, there is a slight preference for the predator to drill the left valve, 55% of those bored being the left ones. There is a more obvious preference in the location on the shells where the borings are made, 75% of the holes drilled in the left valves and 54% of holes in the right valves are located on the anterior slope; the remaining 25% and 46%, respectively, of the borings are located on the disc (see fig. 1). No holes are located on the narrow posterior slope. Most holes are located nearer the umbos dorsally than they are to the ventral margin.

The fact that most boreholes are nearer the dorsal edge of the valve than in any other position indicates feeding behavior of the predator similar to that described by FRETTER & GRAHAM (1962, pp. 572-574). The latter described predation by *Natica* which manipulates the bivalve prey with its foot, turning the bivalve so that it can bore into it in a precise manner. This complexity of behavior

seems to characterize some gastropod predation and especially that entered into by Naticidae (CARRIKER & YOCHELSON, 1968; EDWARDS, 1975; BERG & NISHENKO, 1975).

Location of the boreholes mostly in the dorsal area of valves of the population of *Periploma margaritaceum* may indicate predator preference for boring in that site. Since shells of *P. margaritaceum* are rather uniformly thin, it seems probable that boreholes are made in this area of the shell because it provides the most efficient access to the predator's meal. As pointed out by CARRIKER & YOCHELSON (1968) location of Naticid borings may be limited by the grasping ability of the predator. While that interpretation would place matters of preferences into the category of genetically programmed behavior, it is extremely likely that the grasping ability of the predator has been subject to intense selective pressure favoring most efficient feeding on available prey species.

ANSELL (1960) found *Natica alderi* (Forbes, 1838) to bore preferentially in the ventral regions of the shells of *Venus striatula* (da Costa, 1778). He suggested that one reason for this was that the relatively thick shell of *Venus* is thinnest near the shell margins, outside the pallial line. It appears that in *N. alderi*, also, borehole location is dictated by greatest feeding efficiency. FRANZ (1977) demonstrated that it was the smaller valves of *Spisula solidissima* (Dillwyn, 1817) that were bored by *Lunatia heros* (Say, 1822). Presumably, then, either due to choice or evolutionary pressure, ease of valve penetration may be an important factor in determining where boreholes are made (also see CARTER, 1968: 41).

To detect valve preference and compare locations of predator boreholes in other members of the family Periplomatidae a survey was made of *Periploma margaritaceum* from other localities and seven other species having different shell shapes and sizes. The results are shown in Table 2 and Figure 2. Specimens of *P. margaritaceum* in-

cluded in Table 2 are from lots other than those tabulated in Table 1. Certain tendencies may be noted. In all species most boreholes are located near the dorsal valve margins. Again, in *P. margaritaceum* most holes are in the anterior slope. However, in contrast to the initial lot of *P. margaritaceum*, in this sample, the right valve was bored considerably more often than the left indicating there is variation in the valve chosen by the predator for boring or perhaps variation in which valve is uppermost.

Table 2

Survey of Borehole Locations in Periplomatidae
(see Figure 2)

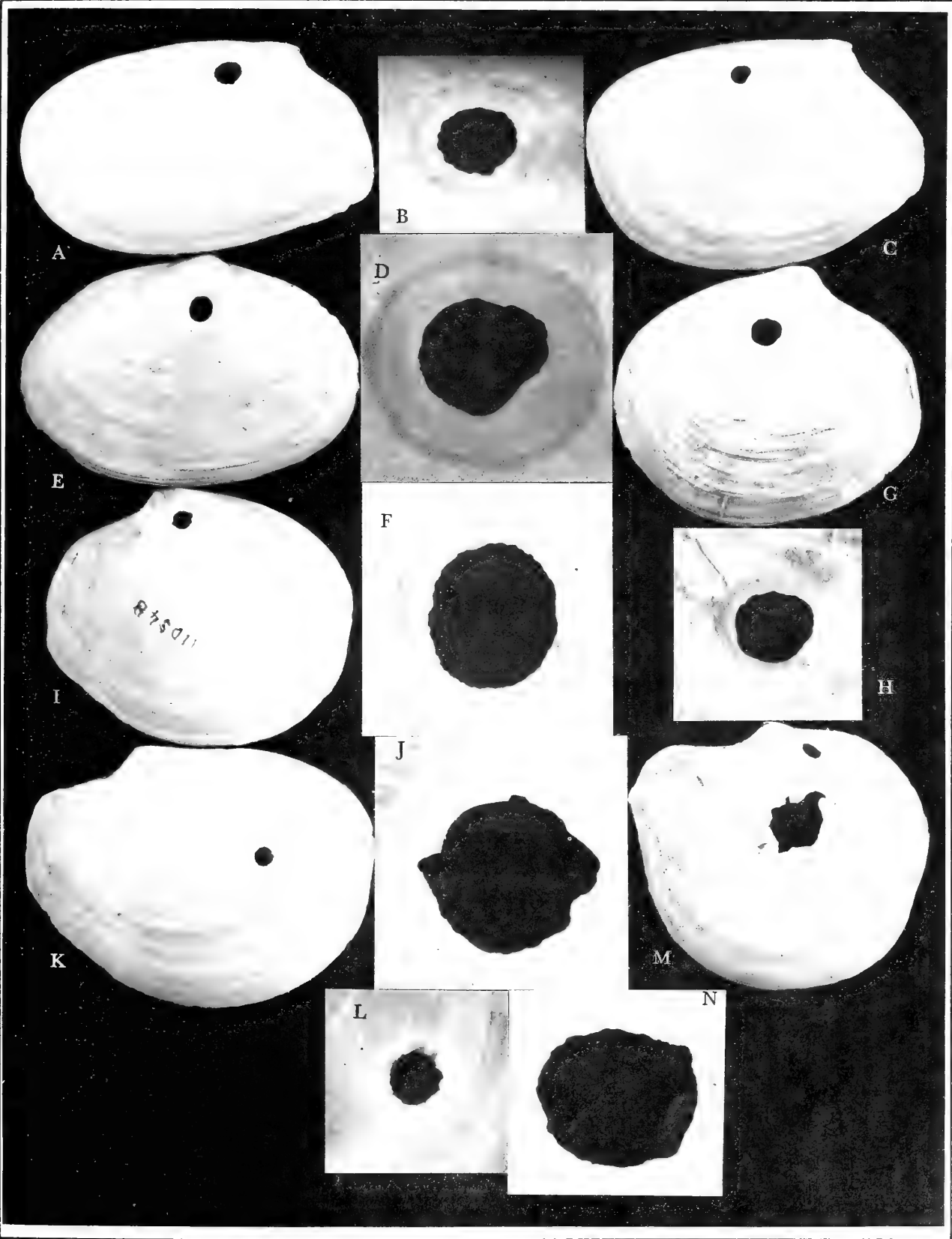
	Valve Bored		Position of Borehole	
	Left	Right	Disc	Anterior Slope
<i>Periploma margaritaceum</i> Lamarck	19	30	3	46
<i>Periploma ovatum</i> Kuroda and Habe		1		1
<i>Cochloidesma leanum</i> Conrad	25	19	40	4
<i>Periploma fragile</i> Totten	13	30	34	9
<i>Periploma stearnsii</i> Dall	1	1	2	
<i>Periploma fracturum</i> Boshoff		1	1	
<i>Periploma discus</i> Stearns	1	1	1	1
<i>Periploma planiusculum</i> Sowerby	2	3	3	2

Of the other species surveyed, specimens of *Cochloidesma leanum* and *Periploma fragile* were numerous enough to give an indication of predator selectivity in boring sites (see Table 2 and Figure 2, E-H). In *C. leanum* there appears to be a slight preference for left valves (57%) versus right (43%) as a site for boring. The area of

Explanation of Figure 2

- A, B. *Periploma margaritaceum* Lamarck, Matagorda Bay, Indianola, Calhoun County, Texas, USNM 465183. A. left valve, length 18 mm; B. borehole, largest diameter (including bevel) 2.5 mm
C, D. *Periploma planiusculum* Sowerby, Dominical, Costa Rica, USNM 597917. C. left valve, length 37.1 mm; D. borehole, diameter 4 mm
E, F. *Cochloidesma leanum* Conrad, south of Gay Head, Martha's Vineyard, Dukes County, Massachusetts, USNM 95546. E. left valve, length 33.7 mm; F. borehole, diameter 3.8 mm

- G, H. *Periploma fragile* Totten, Sand Island, New Brunswick, Canada, USNM 444773. G. left valve, length 14.1 mm; H. borehole, diameter 1.9 mm
I, J. *Periploma stearnsii* Dall, off Point Fermin, Gulf of California, USNM 110548, Holotype. I. right valve, length 44.8 mm; J. borehole, diameter 4.5 mm
K, L. *Periploma fracturum* Boshoff, Anton Bruun Station 391-F, northeast of Durban, South Africa, 77m, USNM 718117. K. right valve, length 17.4 mm; L. borehole, diameter 1.8 mm
M, N. *Periploma discus* Stearns, Long Beach, California, USNM 126931, Holotype. M. right valve, length 43 mm; N. borehole, diameter 3.5 mm



the disc (90%) is clearly more often penetrated than the anterior slope (9%). In *P. fragile* right valves (70%) are more often penetrated than left (30%). The disc (79%) again appears to be the boring site chosen over the anterior slope (21%).

It is not known what predator species were involved in attacking the bivalves surveyed in Table 2, except that the boreholes indicate Naticid predation. No boreholes were found in posterior slopes of any specimens examined in this survey. That area of the shells of periplomatids tends to be truncated, generally reduced in size, and may be in an inconvenient area for penetration by Naticids.

SUMMARY

1. Of 443 valves of *Periploma margaritaceum* from Matagorda Bay, Texas, 185 or 42% were bored by a naticid gastropod, probably *Polinices duplicatus*.
2. In this sample a slightly larger percentage of left valves of *Periploma margaritaceum* is bored than right valves. In a smaller sample of the same species it is the right valve that is more frequently bored.
3. While *Periploma margaritaceum* and other Periplomatids may lie horizontally on one side within the substratum, there is little evidence from location of boreholes as to which side is uppermost.
4. In almost all instances boreholes are made in the dorsal part of the valves, either in the anterior slope or disc. These data are consistent with evidence from other workers indicating that naticid predators manipulate prey and select areas for boring that allow most efficient penetration and feeding.
5. Whereas in *Periploma margaritaceum* the anterior slope is the preferred site of boring, in *Cochlodesma leanum* and *Periploma fragile* it is the disc. This difference may be due to the fact that the former is strongly inequilateral while both *C. leanum* and *P. fragile* are more equilateral than *P. margaritaceum*.
6. No boreholes were noted in the posterior slope, probably due to its small size.

ACKNOWLEDGMENTS

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ceum; H. Harry suggested the identity of the naticid predator.

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Several weeks after returning the galley proofs the following paper appeared:

- WILLIAMS, LORALYNN
1979. Boring and feeding behaviors (sic) of the California marine gastropod *Ceratosoma nuttalli*. Of Sea and Shore 10 (1): 18-20; 3 text figs.

Habitat, Food and Reproductive Activity of the Nudibranch *Hexabranchnus sanguineus* on Tongatapu Island

BY

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(4 Text figures)

INTRODUCTION

THE TAXONOMY OF THE GENUS *Hexabranchnus* Ehrenberg, 1831 is confused and requires revision. More than 20 species have been described (see THOMPSON, 1972), many of them based primarily on differences in colour pattern. Some authors (BERGH, 1900; ELIOT, 1904; THOMPSON, 1972) consider the many named species to be merely colour varieties of *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1828). The validity of the use of colour pattern as a taxonomic character remains to be demonstrated in this genus. Nevertheless, a full description of the colour pattern of Tongan *Hexabranchnus* is given below to facilitate comparative studies in the event that colour does prove to be distinctive. External and internal morphology appear to vary little among the described varieties (ELIOT, 1904) but these features were not investigated in Tongan animals.

In the absence of any distinctive taxonomic characters, Tongan *Hexabranchnus* are here referred to the type species of the genus, *H. sanguineus* (Rüppell & Leuckart). Other described "species" will here be considered simply as colour variations of *H. sanguineus*.

Little work has been done on the biology or ecology of *Hexabranchnus*. The only comprehensive study is that of GOHAR & SOLIMAN (1963) on Red Sea specimens. Several authors have commented on feeding and stomach contents, and a review of their results is presented below. ØSTERGAARD (1950) has described spawning and development in 2 Hawaiian varieties.

The only *Hexabranchnus* previously recorded from Tonga is *H. flammulatus* (Quoy & Gaimard, 1832). Specimens 10 to 13 cm long were collected during the voyage

of the *Astrolabe* from Tongatapu Island (21°10'S; 175°10'W; see Figure 1).

DESCRIPTION

The colour of the dorsum and foot of *Hexabranchnus sanguineus* varied from pale pink to dark red. The general appearance was, however, influenced by the colour, size

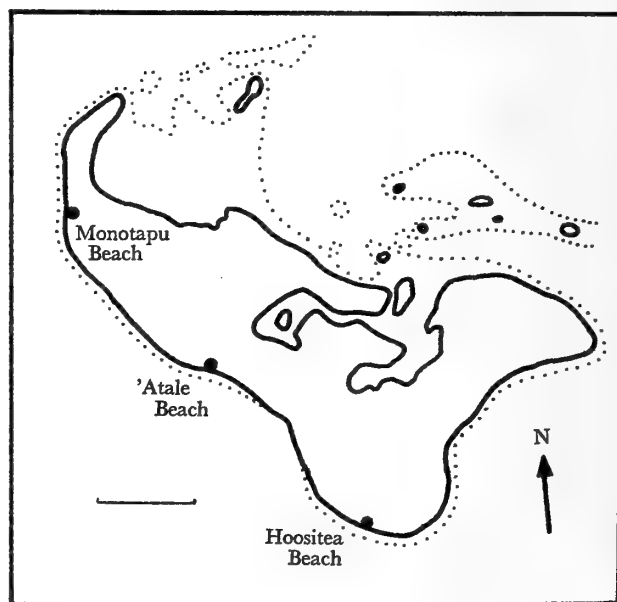


Figure 1

Tongatapu Island, Tonga, showing localities mentioned in the text. Dotted line indicates the edge of the fringing reef. Scale = 5 km

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and density of spots covering the dorsum; these ranged from large dense yellow spots (producing an overall orange appearance) to small white spots (which allowed the background colour to dominate the appearance). Most of the animals seen were dark red with these dense yellow spots on the dorsum (Figure 2, zone A).

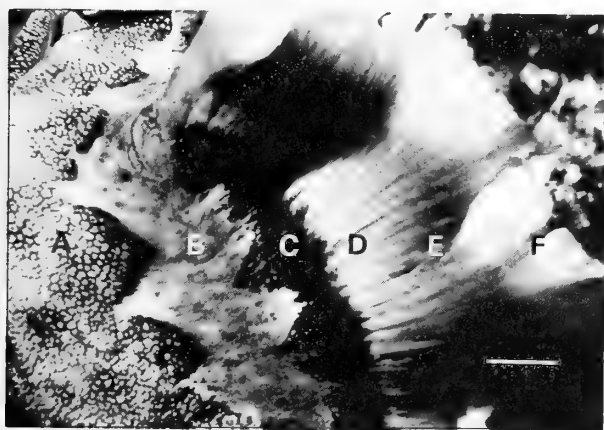


Figure 2

Close-up photograph of a large *Hexabranchnus sanguineus* showing colour zones. See text for explanation of colour pattern of the various zones. Scale = 1 cm

In animals longer than about 6 cm, 5 colour bands were distinguishable on the notum (see Figure 2). Band B was comprised of a translucent layer of white pigment overlying dark red tissue, producing an overall mottled pink band punctuated with red spots. Band C was a dark red colour. Occasionally, band B was interrupted by a dark red intrusion from band C which linked with the dorsum. These intrusions probably represent areas from which the overlying pigment of band B is absent.

Band D was white with dark red lines radiating out from band C. These lines merged to produce a mauve coloured band E. The edge of the notum, band F, was always white.

Animals shorter than 6 cm were very similar to larger animals, except that bands D and E were frequently merged to form a single light purple band.

One small animal (1.8 cm long) had a different colour pattern. The notum had only 3 colour bands: a white margin tinged with blue, a central orange band with violet notches along its distal edge, and an inner white band. This could represent the juvenile colour pattern,

with the number of bands increasing with animal size as the violet notches coalesce to produce the characteristic red and purple bands of all larger animals.

The underside of the notum and the foot were dark red with yellow or white spots.

The rhinophores were red, and spotted with yellow or white, and the lamellae were red with yellow edges. The rhinophore collars were densely spotted with yellow or white and had bright red rings around their distal edges.

The gills were yellow and veined with red.

The only significant difference in colour pattern between Tongan *Hexabranchnus* examined in this study and *H. flammulatus* described by QUOY & GAIMARD (1832: plt. 17, figs. 6 & 7) is the presence in the latter of distinct white pennants punctuated with red adjoining the dorsum. These pennants clearly represent the remains of colour band B after it has been split into segments by dark red intrusions from band C. Distinct segments were not observed in the present study and band B was usually continuous around the whole notum. Distinct segments appear to be a feature of Australian *Hexabranchnus* and are clearly seen in illustrations by GILLET & MCNEILL (1959: plt. 84) and THOMPSON (1972: fig. 2B). Otherwise, Tongan and Australian animals differ little in colour pattern.

Hexabranchnus marginatus (Quoy & Gaimard, 1832) as illustrated by BERGH (1905: plt. 1, fig. 2) has an almost continuous band B and is very similar to Tongan animals. The only visible difference is that band D in *H. marginatus* is yellow in Bergh's figure, although Quoy & Gaimard's original description (1832: 255) gives it as white.

METHODS

During a preliminary survey of the coastline of Tongatapu Island, *Hexabranchnus sanguineus* were found to occur predominantly on the shallow fringing reef platforms all around the island except on the sheltered north coast. The animals were most common on the south and southwest coasts where the fringing reef is approximately 100 m wide. Two sections of reef, at Hoositea Beach and Monotapu Beach (Figure 1), were chosen for further study and were visited regularly between March and November 1976.

HOOSITEA BEACH

A section of reef 100 m long was searched from the beach to the reef rampart (a distance of 125 m) at ap-

proximately monthly intervals between March and October 1976. Searches were conducted at low tide and covered an area of 1.25 hectares. All *Hexabranchnus sanguineus* found within the area were counted and measured to the nearest centimeter below extended crawling length (excluding the foot). This measurement corresponds with the standard mantle length, Am , of RISSO-DOMINGUEZ (1963). Channels in the reef were examined by snorkel diving.

Sea surface temperatures were measured at mid-morning over the low tide period in surge channels just inside the edge of the reef.

Specimens of *Hexabranchnus sanguineus* were collected, cleaned of adhering debris and placed individually in seawater-filled jars which were then submerged in reef channels. After 1 to 5 hours the animals were released and their faeces collected and preserved in neutral formalin.

MONOTAPU BEACH

The inner 85 m of a section of reef 60 m long was searched at least once a month from April to November 1976. Searches were conducted at low tide and covered an area of 0.5 hectare. The outer edge of the reef was not searched because preliminary surveys had shown *Hexabranchnus sanguineus* to be absent from this part of the reef, where a strong current flowed across the reef from the south.

All *Hexabranchnus sanguineus* egg coils found within the area were counted and removed (to ensure that no egg coil was counted in a subsequent search).

Faecal samples were collected from live animals as for Hoositea Beach.

RESULTS

HABITAT

Hexabranchnus sanguineus were abundant on shallow reef platforms on exposed coasts. In one 3-hour period, 45 animals were found in the 1.25 hectare area searched at Hoositea. *Hexabranchnus sanguineus* could only be found readily over the low tide period. At other times they disappeared from view, probably into coral crevices in the reef.

Reef platforms on exposed Tongan coasts are protected from the prevailing south-easterly swells by raised ramparts at their seaward edges. The extent of protection afforded to reef platform organisms depends upon the

state of the tide: during the low tide the water remaining on the reef is calm, whereas at high tide waves break over the rampart producing turbulent conditions.

The rampart at Hoositea shelters the reef for about half of the 12-hour tidal cycle. The reef is almost horizontal in profile and is covered by about 1.5 m of water at high tide. At low tide the reef dries almost completely, except for the numerous channels in the reef. These channels are up to 2 m deep and run at right angles to the beach.

Monotapu has a similar reef structure to Hoositea, but the reef is subject to turbulent wave action for about $\frac{2}{3}$ of the tidal cycle, and does not drain completely at low tide. A layer of water 10 cm to 30 cm deep remains at low tide.

The reef platform around most of Tongatapu Island is composed of compacted fused coral, and covered by a turf of coralline algae. Live coral (mainly *Porites* and *Acropora* species) is rare and confined to the channels which are water-filled at all times. Patches of dead *Acropora* project up to 30 cm above the level of the reef flat.

At low tide, *Hexabranchnus sanguineus* were usually found crawling over the substrate, either among dead *Acropora* branches or on the algal turf. The animals actively avoided live coral, but were frequently seen moving among the algae-encrusted bases of live coral. They were rarely found in the reef channels, but sometimes occurred on the vertical sides of the channels.

Hexabranchnus sanguineus probably shelter in coral crevices over high tide and thus reduce the risk of being swept from the reef or being damaged by the abrasive action of suspended sediment.

The distribution of *Hexabranchnus sanguineus* across the reef was found to be non-random with respect to the size of the animal. The distribution by size was analysed during one low tide sampling period (1 July 1976), and the results are presented in Figure 3. Animals less than 3 cm long occurred only on the outer edge of the reef near the rampart. *Hexabranchnus sanguineus* between 3 cm and 7 cm were found throughout the outer half of the reef, and large animals (exceeding 7 cm) occurred over the whole reef, but were most common on the inner half.

WATER TEMPERATURE

At Hoositea, water covering the outer $\frac{1}{4}$ of the reef platform is continually renewed at all tides by the influx of ocean water through the surge channels in the reef rampart. The outer section of the reef platform is therefore buffered against large diurnal fluctuations in temperature and salinity. The inner $\frac{3}{4}$ of the reef is more subject to temperature changes due to solar heating and

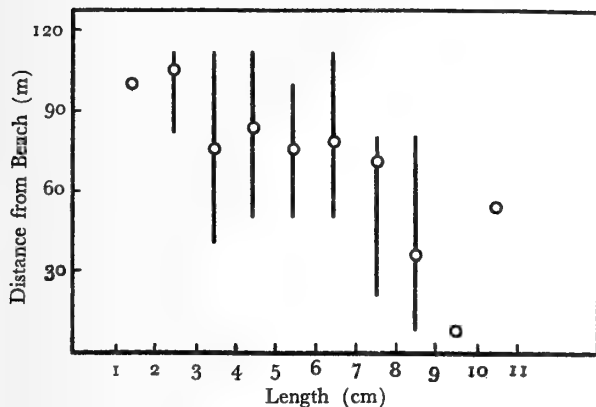


Figure 3

Distribution of *Hexabranhus sanguineus* across Hoositea reef by size ($n=45$). Open circles indicate mean distance of each size class from the beach, and vertical lines indicate the observed ranges. Size classes with no marked range were represented in the sample by only one specimen each

night-time cooling, and salinity changes due to evaporation and freshwater seepage from the beach.

Temperature and salinity conditions at Monotapu are more constant than at Hoositea. The water level over the reef does not drop as low at Monotapu, and ocean water circulates continuously over most of the reef.

Sea surface temperatures measured at Hoositea are plotted in Figure 4, and indicate the trends during the period April to October. Temperatures ranged from 22.5°C to 27.6°C. The highest temperature recorded in the shallow water overlying the inner sections of Hoositea reef was 29.4°C; higher temperatures than this would be expected from January to March.

REPRODUCTIVE ACTIVITY

The egg coils of *Hexabranhus sanguineus* found in Tonga were consistent with the description of GOHAR & SOLIMAN (1963: 230-231). Freshly-laid coils were bright red, fading to a dull red-brown colour as the embryos developed.

The number of egg coils found at Monotapu fluctuated randomly from April to November (Figure 4). Egg coils were found in varying numbers during the coldest months, but apparently disappeared as the water temperature started increasing again. The absence of samples from the hottest part of the year precludes a full comparison of reproductive activity with seawater temperature.

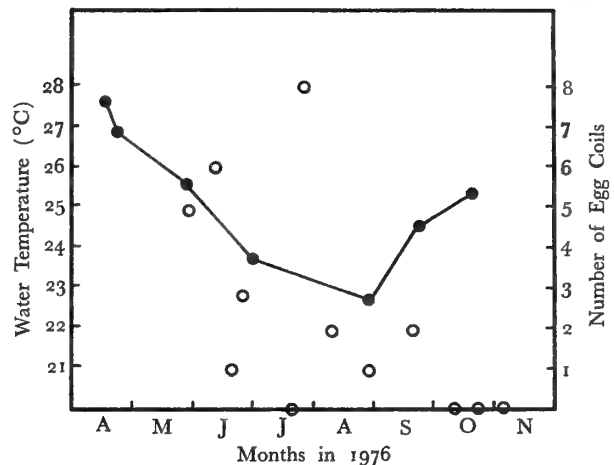


Figure 4

Number of egg coils of *Hexabranhus sanguineus* found at Monotapu (open circles) and sea surface temperature measured at Hoositea (closed circles)

Hoositea was less preferred as a breeding site than Monotapu. Only 2 egg coils were found at Hoositea despite the much larger area searched throughout the study period.

SIZE STRUCTURE OF THE HOOSITEA

POPULATION

The size-frequency distributions of the Hoositea *Hexabranhus sanguineus* samples are shown in Table 1. Very small individuals were probably present throughout the study period, despite their absence from the first 2 samples. An animal 1.8 cm long was found at 'Atele Beach (Figure 1) on 19 April 1976, and a 1.5 cm animal (the smallest found in this study) at Hoositea on 24 April 1976. Even the 1.5 cm long animal was able to flare its notum when disturbed, and was able to swim. Large adults were present throughout the study, although none larger than 14 cm was found.

Most of the large samples had unimodal size-frequency distributions with modes between 5 cm and 7 cm. Small size classes have probably been under-represented because of their cryptic coloration. Since animals less than 4 cm were present from April to October, it appears that larval settlement on the reef occurs throughout this period. Larval settlement was especially heavy some time prior to the sample of 29 May 1976, as this sample contained

Table 1

Size-frequency distribution of samples of *Hexabranchnus sanguineus* taken at Hoositea Beach.

Date of sample in 1976	Length (nearest cm below)													Number in sample
	1	2	3	4	5	6	7	8	9	10	11	12	13	
14 March					1		3	2		1	1	2		10
18 April			1	1	2	3	1	1	1		3	1	2	16
29 May	2	3	1	1	4	5	2	4	4	2	1	1		30
1 July	1	5	5	5	7	9	7	4	1	1				45
30 July			3	6	8	5	6	1	1		1			31
30 August		2	2	4	8	9	7	6	3		1		1	43
26 September			2	2	4	2	1	3	2	3	2	1	1	23
22 October			1	2	3	4	7	5	1	2	1		1	27

many small animals. The strong size class could also be detected in subsequent samples.

Few animals longer than 10 cm were found.

FEEDING

An examination of faecal material showed that *Hexabranchnus sanguineus* feeds on sponges. All of the 13

faecal samples collected contained a large proportion by volume of sponge spicules. The species eaten, based upon spicule identification of 6 faecal samples, are shown in Table 2. *Hexabranchnus sanguineus* feeds on at least 11 genera of sponges from 5 orders and 2 classes, and is clearly a non-selective browser.

A wide variety of non-sponge material was also identified from the faeces. Non-sponge components of the gut contents found in this study and by other authors are listed in Table 3. This material never formed more than a small proportion of the faecal material of Tongan animals.

Table 2

Sponge species identified from faeces of *Hexabranchnus sanguineus* and their frequency of occurrence.

Sponge species	Number of animals in which sponge was found (n = 6)
CALCAREA	
Calcareous triradiates	2
DEMOSPONGIAE	
CHORISTIDA	
<i>Stelletta</i> sp.	1
<i>Ancorina acervus</i> (Bowerbank)	1
<i>Pachastrella</i> sp.	1
HADROMERIDA	
<i>Cliona</i> sp.	3
HAPLOSCLERIDA	
<i>Haliclona</i> sp. or <i>Adocia</i> sp.	2
<i>Callyspongia</i> sp.	3
POECILOSCLERIDA	
<i>Xestospongia exigua</i> (Kirkpatrick)	1
<i>Petrosia</i> sp.	5
<i>Paraesperella</i> sp.	1
<i>Mycale</i> sp. or <i>Zygomycale</i> sp.	4

Table 3

Non-sponge material identified from faeces of *Hexabranchnus sanguineus*.

Material	Source
Algae	ABOUL-ELA (1959); GOHAR & SOLIMAN (1963); present study
Foraminifera	EALLES (1938); GOHAR & SOLIMAN (1963); present study
Hydroids	BERGH (1900); ELIOT (1906)
Alcyonarians	GOHAR & SOLIMAN (1963)
Coral fragments	GOHAR & SOLIMAN (1963); present study
Worm tubes	BERGH (1900); EALLES (1938); present study
Gastropod shells	EALLES (1938); present study
Amphipods	Present study
Crab chela	Present study
Polyzoans	ELIOT (1906)
Echinoderm shells	EALLES (1938)
Ascidian spicules	THOMPSON (1972)

DISCUSSION

REPRODUCTIVE ACTIVITY

Red Sea populations of *Hexabranchnus* continued to breed throughout the year but activity declined during the cold months (GOHAR & SOLIMAN, 1963). The number of egg coils at Monotapu showed no relationship to seawater surface temperature during the 8 months of observations (Figure 4). GOHAR & SOLIMAN (1963: 242) believe that spawning in *H. sanguineus* is induced by increasing temperatures following winter low temperatures. The minimum temperatures in the Red Sea (16°C to 19°C [GOHAR & SOLIMAN, *loc. cit.*]) were considerably lower than the lowest temperature measured during the Tongan winter (22.5°C), and it is possible that the temperature of Tongan waters is suitable for uninterrupted year-round breeding.

The scarcity of egg coils at Hoositea was probably due to unfavourable environmental conditions. The temperature of water trapped in channels at low tide during the day increases and the dissolved oxygen concentration probably decreases. GOHAR & SOLIMAN (1963) observed retardation of embryo development in stagnant water. Egg coils kept in a non-circulating aquarium in this study disintegrated before larvae were ready to hatch. The continual renewal of seawater at Monotapu produces a more constant environment for larval development than exists at Hoositea.

FEEDING

Hexabranchnus sanguineus is a sponge feeder, consuming a wide variety of species. The sponges taken are mainly inconspicuous encrusting species, probably occurring in crevices and holes in the reef matrix (P. Bergquist, personal communication). Most other workers have also recorded sponges in the diet of *Hexabranchnus*. BERGH (1900: 231) found "fragments of transparent spicules" and "masses of simple and three-rayed silica needles" in one specimen; these were obviously sponge remains. ELIOT (1906) and GOHAR & SOLIMAN (1963) noted that sponges form at least part of the diet of *Hexabranchnus*, and YOUNG (1966) reported the calcareous sponge *Leucetta solida* from the gut of a Hawaiian specimen. KAY & YOUNG (1969) concluded that 3 Hawaiian varieties of *Hexabranchnus* were "rasping sponge feeders."

The wide variety of non-sponge material in the gut contents of the different varieties of *Hexabranchnus* is indicative of an indiscriminate mode of feeding. The ani-

mals ingest much extraneous material while feeding on the encrusting sponges in the crevices where other organisms, animal skeletons and detritus also collect.

The contention that *Hexabranchnus* is entirely herbivorous (ABOUL-ELA, 1959) is not supported. It is likely that algae are ingested accidentally during feeding, and they appear to pass through the gut undigested.

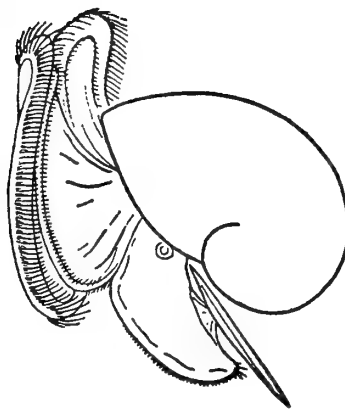
BLOOM (1976) has demonstrated a correlation between the radula and digestive morphology of dorid nudibranchs, and the type of sponge preferred as prey. Bloom's major thesis is that the presence of a gut caecum (a spicule-compacting organ) enables nudibranchs to handle large quantities of large sharp spicules, and they are therefore adapted to feeding on sponges with unorganised or non-reticulated skeletons. Conversely, nudibranchs lacking a gut caecum, but possessing a robust radula, are able to feed on, and digest, sponges with organised, reticulated skeletons. The only sponge prey of *Hexabranchnus marginatus* mentioned by BLOOM (1976: table 3) is *Leucetta solida*, originally reported by YOUNG (1966). Thus, using limited data, Bloom finds that *Hexabranchnus*, which possesses a caecum and radula teeth with a low degree of hook (Bloom's measure of tooth robustness) feeds on non-reticulated sponges; this supports his contention that a correlation exists between nudibranch morphology and sponge prey. However, the present study has shown that *H. sanguineus* consumes a wide variety of sponge types, ranging from unorganised non-reticulated sponges (calcareous species) to highly organised reticulated species (*e. g.*, *Mycale* sp., *Petrosia* sp., *Callyspongia* sp.) (see BLOOM, 1976: table 1, for a description of skeletal structure in each of these groups). The presence of a gut caecum may indeed allow *Hexabranchnus* to feed on non-reticulated sponges, but the absence of robust radula teeth does not prevent it from also eating reticulated sponges. Generalist sponge feeders are exceptions to Bloom's correlations, and other species may also prove to be generalists on closer study.

ACKNOWLEDGMENTS

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Depth Distribution of *Nautilus pompilius* in Fiji and *Nautilus macromphalus* in New Caledonia

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(1 Plate; 6 Text figures)

INTRODUCTION

AMMONITE WORKERS have long noticed that adults and juveniles of the same species are often segregated by facies. This observation indicates either selective preservation, selective post-mortal drift, or that different growth stages were separated geographically or by depth. KENNEDY & COBBAN (1976) have discussed this problem in their review of ammonite paleobiology, and have concluded that at least in some instances the latter hypothesis has been valid. It was therefore suggested that significant migration must have occurred during the lifecycle of some species.

Migration for feeding or breeding is well-known in many coleoid cephalopods (PACKARD, 1972), but has been little examined in Recent *Nautilus*, which, because of its greater morphologic similarity to the ammonites than the coleoids, is probably a more useful analogue. We have examined the depth and geographic distributions of 2 species of *Nautilus*, *N. pompilius* in the Fiji Islands, and *N. macromphalus* in New Caledonia. The results of these observations, reported in this paper, indicate that separation of adults and juveniles occurs within these 2 populations. Our interpretation of reasons for this segregation in *Nautilus* may have some applicability in interpreting distribution patterns of ammonites.

METHODS AND CAPTURE SITES

The captures of *Nautilus* were accomplished using methods previously described by WARD *et al.*, 1976. The use of hydraulic winches and sophisticated bottom sounding gear in Fiji, donated by the department of Fisheries, Fiji, enabled us to set traps to depths of 750 m. In New Caledonia, trapping efforts were conducted on small private boats without the benefit of winches, and hence were severely limited as far as depth capabilities. No trapping from depths greater than 100 m was attempted.

The reef environments and trapping areas in Fiji have been previously described (WARD *et al.*, 1977). In New Caledonia, all captures have been made at one area on the barrier reef fore-reef slope near Noumea (Figure 1). Seaward of the 10 m wide algal ridge the reef flat extends into a zone of actively growing coral heads which are dissected by spur and grooves perpendicular to the reef crest. This zone is several hundred meters wide and descends to a depth of 10 to 15 m, where a pronounced break in slope occurs. A steep scarp, descending to depths varying between 40 and 50 m, is covered with growing coral in the upper half, but shows mainly algae in the lower portions. At the base of this reef precipice is a talus slope of reef rubble and sand, with little actively growing coral. The talus slope extends downward to a flatter

terrace of coralline sand and low, hummocky ridges of rubble and algae which commence at depths between 80 and 100 m. All of our trapping in New Caledonia has been from the reef talus and the deeper coralline sand terrace.

RESULTS

In Fiji we captured 57 *Nautilus* from known depths and positions during 1976 and 1977. These specimens have been separated into groupings by depths and compared (Figure 2). Twenty-five specimens from depths between 100 and 300 m had an average weight (in air) of slightly less than 500 g. No specimens of less than 300 g total weight were captured. Thirty-two specimens from depths greater than 300 m had a mean weight of 413 g, and 9 animals of less than 300 g were captured. If these assemblages were to be preserved in the fossil record, we would see a shallower facies with no juveniles, and a deeper facies with both juveniles and adults.

In Fiji, the deepest captures were from depths of 600 to 650 m. Traps were placed at 700 m on 5 occasions, with no *Nautilus* captures resulting. The maximum habitat depth of *Nautilus* is dictated at least in part by the strength of the shell against implosion, and to study this depth limit a number of implosion experiments has been made in pressure devices. DENTON & GILPIN-BROWN (1966) imploded shells at pressures of 53-73 atms., equivalent to depths between approximately 500 and

Figure 1 Data: Number of Specimens by Weight Bin and Sex

Weight Bin (g)	Unsexed	Females	Males	Total
100-150	1	0	0	1
150-200	0	1	1	2
200-250	1	0	0	1
250-300	1	2	2	5
300-350	1	1	0	2
350-400	3	0	1	4
400-450	3	2	0	5
450-500	3	3	2	8
500-550	0	1	6	7
550-600	0	0	3	3
600-650	0	0	3	3

Statistics:
 $n = 32$, $\bar{x} = 413.2$ g
 $\varphi = 0.26\% \bar{x}_f = 360.7$ g
 $\sigma = 0.74\% \bar{x}_m = 478.3$ g

Nautilus pompilius 100-300 m

$n = 25$, $\bar{x} = 498.2$ g

$\sigma = 0.71\%$, $\bar{x}_m = 539.0$ g

$\sigma = 0.29\%$, $\bar{x}_l = 400.5$ g

Number of Specimens

10

5

100 300 500 700

Total Weight (g)

Size-sex distributions of *Nautilus pompilius*, Fiji Islands (Suva Harbor region). The upper group was captured in depths between 300 and 600 m; the lower from depths of 100 to 300 m

700 m. RAUP & TAKAHASHI (1966) and SAUNDERS & WEHMAN (1977) arrived at similar figures. In Fiji we inadvertently imploded the shells of 6 living animals, but at a depth greater than any of those produced experimentally in pressure chambers. The newly captured specimens were lowered in a trap and buoy system to 700 m. One day later, during recovery, we noted that the trap had moved downslope into deeper water. The new resting depth of the trap was deeper than the maximum working depth of the echo sounder on board the recovery vessel, so no measurement of the actual depth was obtained. It

is estimated that the trap was in a depth between 800 and 900 m, however, because only 1000 m of line was attached, and between 100 and 200 m of this was slack on the surface. Retrieval showed that the shells of all animals had imploded (Figures 7A to 7D). In a second experiment, 2 animals were lowered to the maximum depth of the echo sounder, 750 m, and left on the bottom in a closed trap for one hour. Both animals were intact and healthy on recovery, with no apparent excess of cameral liquid. These observations, coupled with our distributional data, indicate that the maximum depth of habitat is probably between 600 and 700 m, and that depths much in excess of 800 m will implode the shells.

The patterns of shell breaks (Figure 7) in the imploded shells are remarkably similar. In each shell both umbilical calyces are preserved. The body chambers were broken into large, curved portions. The external shell surrounding the final phragmocone was also preserved, but in smaller pieces than the body chamber fragments. In each shell the septa were completely fragmented, and sheared to the edge (suture) of the external shell. No pieces of septa were recovered from the trap (mesh size approximately 5 mm), indicating that the force of implosion was violent, breaking all septa and fragmenting the external shell.

There is some evidence that *Nautilus macromphalus* in the New Caledonian region are also size segregated according to depth. Most specimens captured at depths of 100 m or less are mature (*i. e.*, approximated septa, black band around the apertural margin), and have a mean weight of about 650 g. Size and sex distributions of *N. macromphalus* captured during the periods of December-January, 1970-71 and June-July, 1972 are shown in Figure 3. All of these captures were made at depths between 50 and 100 m. There appear to be no significant size or sex ratio differences between the summer and winter captures. As in all other collections of *Nautilus* known to us, males far outnumber females, and no juveniles of less than 100 g total weight were captured. Catches from the deep water trapping show a much smaller average size (P. Rancurel, personal communication, 1977); of a dozen specimens captured to date by ORSTOM deep water trapping (in excess of 300 m) none was mature. The largest was 500 g, and most were between 200 and 400 g.

WILEY (1902) first indicated that *Nautilus macromphalus* in the region of New Caledonia come into shallow water at night, presumably to feed. This early, and previously unsubstantiated observation has been widely quoted, and misquoted, in subsequent discussions of Recent and fossil cephalopod behavior, and has been influential in interpretation of mode of life of fossil forms (see HEPTONSTALL, 1970).

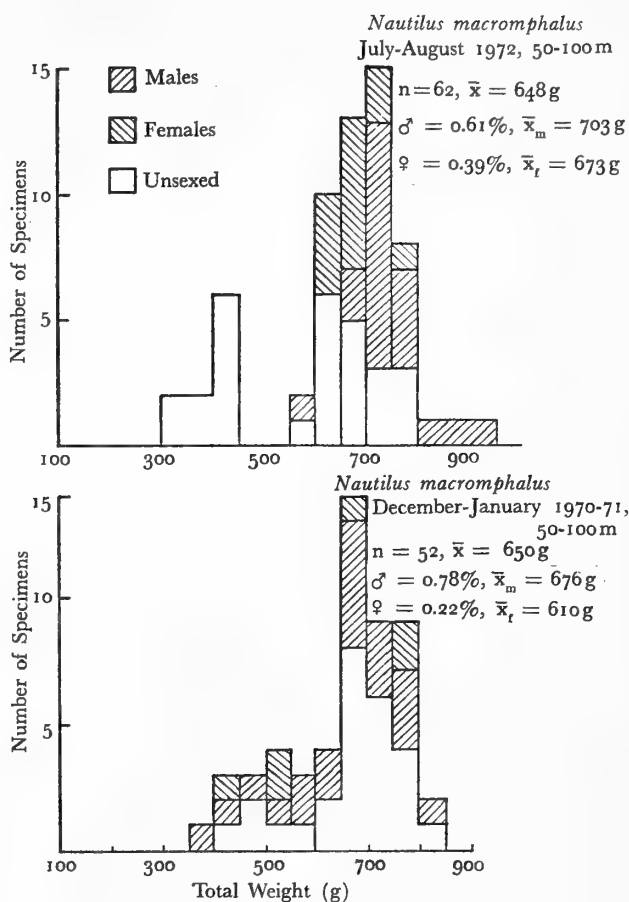


Figure 3

Size and sex distribution of *Nautilus macromphalus* from Récif To, New Caledonia, during the periods July and August, 1972, and December and January, 1970-1971. All captures from 50 to 100 m depth

We have captured 7 specimens at night while SCUBA diving outside the barrier reef over 2 years' time, and none has weighed less than 500 g. Two of these specimens were discovered in water between 5 and 10 m deep in the shallow reef platform environments, several hundred meters offshore of the algal ridge. The other 5 *Nautilus* (September 1977) were captured in depths between 20 and 50 m on the talus slope below the reef scarp. All were found swimming singly. According to the chief diving officer in New Caledonia, nocturnal sightings of *N. macromphalus* by divers are common during the

austral winter months, but are never made during the austral summer months. This lack of shallow water sightings during the summer months may be due to elevated surface temperatures at this time. We have kept *N. macromphalus* in the Aquarium de Nouméa at various times of year, in varying temperatures, and have noted that seawater temperatures above 25° C adversely affect the animals. When the seawater in the aquarium reaches 27° C, the animals die. Surface temperatures outside the barrier reef at our trapping areas usually exceed 26° C during the interval of December to March, whereas depths greater than 100 m have similar water temperatures during all times of the year (Figures 4, 5).

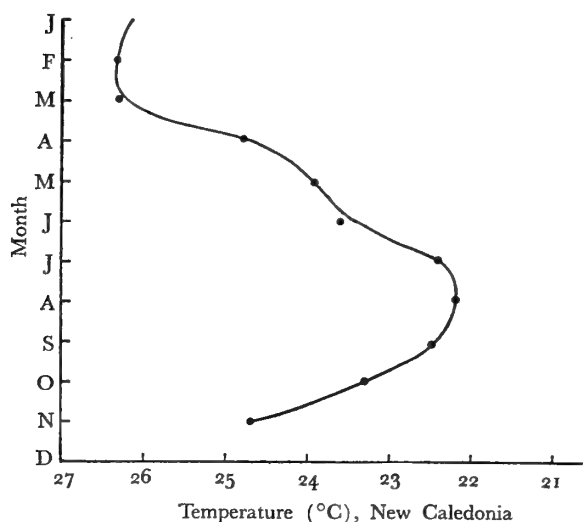


Figure 4

Monthly surface temperatures from Récif To, 1973

The distribution of *Nautilus pompilius* in the Fiji Islands is somewhat different from that of *N. macromphalus* in New Caledonia, in that no fore-reef observations or captures of *Nautilus* are known in Fiji from depths less than 100 m. Shallow feeding migration to near surface waters have never been observed.

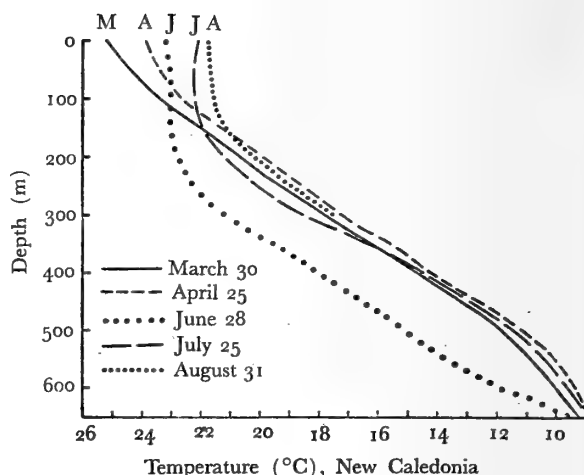


Figure 5

Temperatures at various depths at Boulari Pass, New Caledonia. These temperatures were taken during 1977 outside the barrier reef system near Recif To

WARD *et al.* (1977) trapped systematically from shallow depths of the fore-reef slope environments to depths of 600 m in Fiji, and found that the largest concentrations of *Nautilus* can be captured in excess of 300 m. No specimens were captured in less than 100 m depths, which, in New Caledonia, have proved to maintain significant numbers of *N. macromphalus*. This difference between the 2 areas can probably be attributed to temperature differences. Although little temperature data are available for our sampling site in Fiji, we do have a recent depth/temperature survey for the month of May (Figure 6) which shows significantly higher water temperatures in the shallower depths of Fiji as compared to New Caledonia during the same month. These high temperatures probably account for the lack of sightings of *Nautilus* in shallow water in Fiji.

Explanation of Figures 7A to 7D

- A. Freshly imploded *Nautilus pompilius*
- B. Body chamber fragments × ½
- C. Phragmocone fragments. Note that septa have been evenly removed to suture by force of implosion × ½
- D. Umbilical calyces. Septa evenly removed as in C × 1

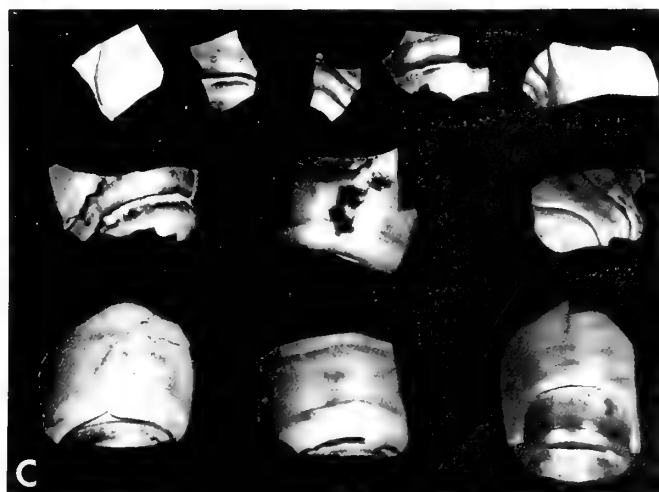


Figure 7

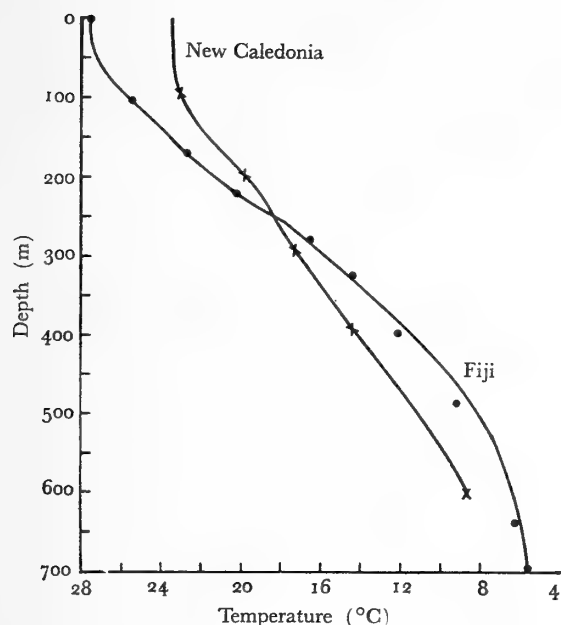


Figure 6

Temperatures at various depths during May, 1977, in New Caledonia (Boulari Pass) and Suva Harbor, Fiji

DISCUSSION

The data presented above, although few in number, strongly suggest that some type of size-depth segregation takes place in these 2 *Nautilus* populations. In Fiji, adult animals are seemingly distributed at all depths. Smaller animals, however, are more common in depths in excess of 300 m. In both New Caledonia and Fiji, the smallest individuals yet captured (less than 200 g) have come from depths in excess of 400 m.

Several lines of evidence have recently suggested to some workers that egg-laying and early development by *Nautilus* takes place in near-surface waters, and possibly even within the lagoon environment. For instance, HAMADA & MIKAMI (1977) have postulated that *N. macromphalus* migrates into shallow water for egg-laying purposes. Eggs are thought to be laid and hatch in depths as shallow as 5 m. Evidence for this hypothesis comes from oxygen isotopic measurements (EICHLER & RISTED, 1966), indicating that early shell secretion takes place in temperatures between 25 and 30°C; and from the only known observations of apparently newly hatched *Nautilus*, seen

in intertidal depths in Fiji within the lagoon (DAVIS & MOHORTER, 1972).

In spite of the arguments above, we favor an alternative hypothesis of a deeper water reproductive site (at least 100 m), for the following reasons. First, it is difficult to believe that juveniles hatch and spend the early parts of their lives in a reef environment at near-surface depths, in temperatures which would be lethal at least to adults. In addition to high temperature, these shallow water sites are also subjected to occasional drops of salinity, due to heavy rain, and to heavy surf and surge during most times of the year.

Secondly, we, and a number of other workers, have maintained *Nautilus* eggs in aquaria at surface temperature and pressure during several years' time, with never a successful hatching. Even though copulation is common, and the eggs are commonly laid in the aquarium situation, they are never fertile, suggesting either sperm or egg inactivation due to adverse environmental conditions, which are most probably due to unfavorable temperatures or pressure.

Finally, if the *Nautilus* were breeding and hatching in shallow reef environments we should expect some sighting of them. In New Caledonia and Fiji numerous divers and shell collectors are perpetually searching the shallow reef for shells, yet other than the observation of Davis and Mohorter, there is no record of any juveniles from these areas, even though large populations of adults can be trapped immediately offshore in deeper water. In our collections, the smallest individuals are invariably in the deepest traps, suggesting to us a deeper water development and early habitat.

The maximum depth from which *Nautilus* has been captured in both New Caledonia and Fiji is 600 m. DENTON & GILPIN-BROWN (1966) raised questions about the accuracy of earlier reports of *Nautilus* from these depths, and suggested that the nature of the cameral liquid removal system may exclude animals in the process of forming new chambers from depths greater than 250 m, since the osmotic gradients maintained between blood and fresh water could only balance a hydrostatic pressure encountered at that depth. CHAMBERLAIN (1978) postulated that immature *Nautilus* would also be found in shallower depths with warm water, since he concluded that cameral liquid could be removed more efficiently in these environments due to permeability properties of the siphuncle. Based on our experience, the observational data are insupportive of these hypotheses. In both Fiji and New Caledonia a number of *Nautilus* has been captured showing evidence of very recent septal formation (thin septa, final chamber filled with cameral fluid of seawater

osmolarity) from depths as deep as 500 m, indicating that cameral fluid formation can and does occur near the maximum habitat depth of the animal. Osmotic gradients sufficient to balance hydrostatic pressure depths greater than 250 m are therefore accomplished in *Nautilus*, indicating that supersaturation of salt in the siphuncular epithelium is occurring.

In conclusion, it appears that in at least 2 populations of *Nautilus*, some size segregation is occurring, with the immature animals in deeper water, and further from shore. Although these deep-water (>300 m) samples also contain some mature adults, they differ markedly from shallower samples which have yielded mainly mature adults. This situation somewhat resembles that described by KENNEDY & COBBAN (1976) for the Western Interior Cretaceous, where young ammonites have been found in deeper, more offshore facies than adults. The reasons for these segregations may be similar in both cases. CHAMBERLAIN (1978) suggests that juvenile *Nautilus* would have a difficult time swimming in the high-turbulence of shallow reef areas. Deeper depths could be expected to be much less turbulent. Secondly, predation pressure by large carnivores, notably reef-fish, moray eels, sharks, and sea-snakes may be more pronounced in shallow reef areas. It could be that juvenile ammonites also sought deeper, offshore areas of lower turbulence and predation pressure.

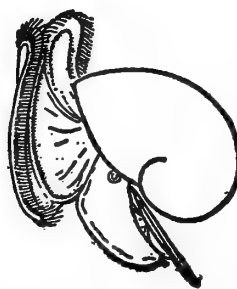
ACKNOWLEDGMENTS

Our research would not have been possible without the support of a large number of people. Dr. and Mrs. Catala, and later Dr. Y. Magnier of the Aquarium de Nouméa

provided aquarium facilities in New Caledonia. Temperature data for New Caledonia were provided by Drs. P. Rougerie and Y. Magnier of O. R. S. T. O. M. Temperature data for the Fiji Islands were provided by Mr. Robert Stone. Diving assistance in New Caledonia was provided by Pierre Laboute and Pierre Djemaoun.

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Notoacmea gabatella (Berry), An Outer Coast Form
of *Notoacmea depicta* (Hinds)

(Mollusca : Acmaeidae)

BY

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(1 Plate)

INTRODUCTION

THIS PAPER WAS ORIGINALLY intended as a short note redescribing, illustrating, and reporting the occurrences of Recent specimens of *Notoacmea gabatella* (Berry, 1960), with the hope that workers, made aware of its rarity, might determine if it is extant, for the last reported specimens were collected in the 1930's or 1940's. However, my plan was changed when I found a small piece of body tissue adhering to the shell of a museum specimen of *N. gabatella* (SDMNH 48479). The tissue contained a portion of the radula. This proved to be virtually identical to that of *Notoacmea depicta* (Hinds, 1842). The specimen was part of the original lot and even had been considered a paratype by some authors. Therefore, I consider *N. gabatella* to be an oval form of the otherwise laterally compressed *N. depicta*. PILSBRY in 1891 had identified a USNM specimen of this oval form as *N. depicta*, but most other workers have not accepted his identification.

Acmaeid limpets that have several *situs* forms are common (cf. McLEAN, 1966; JOBE, 1968; LINDBERG, 1979). However, those occurring on marine plants and algae tend to have highly specialized shell and radular morphologies that limit their success on non-host substrata. Previously only one species occurring on a marine angiosperm was known to have both oval and compressed forms – *Patelloida pustulata* (Helbling, 1779), widely distributed in the Caribbean and in the Gulf of Mexico. The compressed form occurs on the turtle grass *Thalassia testudinum* Banks, 1805, while the oval form occurs on calcium carbonate substrata (e. g., coral heads, encrusting

coralline algae). Several species occurring on algae also have both compressed and oval forms that correspond respectively to branching and encrusting coralline species. These species include *Collisella triangularis* (Carpenter, 1864) and *Acmaea rosacea* Carpenter, 1864. At one time *Notoacmea testudinalis* (Müller, 1776) was thought to have both oval and compressed forms, the former occurring on rocks, the latter on *Zostera marina* Linnaeus, 1753. However, JACKSON (1907) studied the radulae of both forms and demonstrated that the *Zostera* form is distinct. Although this species, *Collisella alveus* (Conrad, 1831), is now separated generically as well (McLEAN, 1966), some workers continue erroneously to list it as a form of *N. testudinalis* (e. g., ABBOTT, 1974).

DALL (1871) was one of the first workers to recognize and illustrate the species-specific nature of the acmaeid radula. GRANT (1937) furthered this work when she studied and illustrated the radular ribbons from over 50 acmaeid species. FRITCHMAN (1960) used radular characters to distinguish his *Acmaea paradigitalis* [= *Collisella strigatella* (Carpenter, 1857)] from both *C. digitalis* (Rathke, 1833) and *C. pelta* (Rathke, 1833). McLEAN (1966; in KEEN, 1971; in MARINCOVICH, 1973) studied the radulae of almost all of the eastern Pacific species and found no species that shared identical radular morphologies or had variations that overlapped or intergraded with another species. LINDBERG (1979) has used radular characters to identify 5 distinct *situs* forms of *C. ochracea* (Dall, 1871). Thus, the acmaeid radula is a powerful tool for resolving taxonomic difficulties encountered in the convergent and highly variable shell morphologies found in acmaeid limpets.

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I am indebted to James T. Carlton, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, who suggested the original topic and provided suggestions and criticisms as the topic evolved. George L. Kennedy, U. S. Geological Survey, Menlo Park, California, supplied a list of the invertebrate fauna of LACMIP locality 332, and provided substantial input in this paper, especially the paleoecology section, for which I am most grateful. Michael G. Kellogg, Moss Landing Marine Laboratories, Moss Landing, California and James H. McLean, Natural History Museum of Los Angeles County, Los Angeles, California, also provided criticisms of the manuscript. Hans Bertsch, San Diego Museum of Natural History, San Diego, California, Barry Roth, California Academy of Sciences, San Francisco, and Edward C. Wilson, also of the Natural History Museum of Los Angeles County, loaned specimens from their respective institutions.

ABBREVIATIONS USED

The following abbreviations are used herein:

- ANSP – Department of Mollusks, Academy of Natural Sciences, Philadelphia, Pennsylvania
 CASG – Department of Geology, California Academy of Sciences, San Francisco, California
 LACMIP – Section of Invertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California
 MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
 SU – Department of Geology, Stanford University, Stanford, California (now on permanent loan to CASG)
 SDMNH – Department of Marine Invertebrates, San Diego Museum of Natural History, San Diego, California
 UCMP – Department of Paleontology, University of California, Berkeley, California
 USNM – Division of Mollusks, U. S. National Museum of Natural History, Washington, D. C.

HISTORICAL REVIEW

The first known oval specimens of *Notoacmea depicta* ("*Acmaea*" *gabatella*) were both collected live at San

Diego, California and were catalogued into the USNM collection in 1885 (*ex* R. E. C. Stearns Collection). In the first report on the specimens PILSBRY (1891) illustrated the larger specimen, identifying it as an oval form of *N. depicta*. Pilsbry's treatment of the specimen may have been influenced by remarks concerning *N. depicta* made by DALL (1871) who predicted, "It is quite likely that thorough dredging would result in procuring non-compressed specimens, which might have grown on pebbles, & c., ..." Pilsbry's conclusion clearly confirms this prediction.

Two more specimens collected from "kelp leaves, stems" at San Pedro, California, were originally identified as "young *Acmaea scabra*." This is undoubtedly intended as *Acmaea scabra* (Reeve, 1855), now considered a synonym of *Collisella limatula* (Carpenter, 1864); the name was rejected by DALL (1914) as a secondary homonym. The specimens were probably collected in the early 1900's and identified prior to Dall's publication.

Avery Ransome Grant, working on her doctoral dissertation, considered these oval specimens in the USNM collection distinct from *Notoacmea depicta* and not forms of it as suggested by PILSBRY (1891). However, this is evident only by a note left with one of the specimens, "not *Acmaea depicta* probably not an *Acmaea* (*teste* A. R. Grant)"; no mention of the specimens appeared in GRANT's thesis (1937) or subsequent publications (TEST, 1945; 1946). Another (undated) note left with the specimen reads, "this may be a *Helcion* E.P.C." (E.P.C. = Emery Perkins Chace of Lomita, California). The reasoning for this is not clear to me. *Helcion* deMontfort, 1810, is a patellid genus characterized by a submarginal apex, a character which the specimen clearly lacks.

A series of specimens (at least 7) was dredged by A. M. Strong off Reef Point and Laguna Beach, California. The exact date(s) is(are) unknown, but was(were) probably between 1930 and 1945. After Strong's death his collection went to SDMNH where the specimens were examined and subsequently described by S. Stillman Berry as "*Acmaea*" *gabatella*.

In 1963, Roger D. Reimer and George P. Kanakoff collected unconsolidated fossiliferous sediments from a cut bank in the 600 block of Miraflores Street, San Pedro, California (LACMIP loc. 332). From this material over 100 specimens of the oval form were recovered making it one of the more abundant "species" in the Pleistocene fauna.

McLEAN (1966) considered "*Notoacmea gabatella*" as part of his doctoral dissertation. McLean was the first worker to recognize the Recent specimens from San Pedro

as "*N. gabatella*" and illustrated Berry's type material for the first time. He was also the first worker to recognize the Pleistocene specimens as "*N. gabatella*."

WILSON & KENNEDY (1967) listed all of the Strong specimens of "*Notoacmea gabatella*" at SDNMH as type material and gave the same locality, Reef Point, for all 7 specimens. However, only 2 specimens are from Reef Point and only these were designated as type material by BERRY (1960). The remaining 5 specimens from Laguna Beach are not types.

ABBOTT (1974) suggested that "*Acmaea gabatella*" may be an aberrant form of *Notoacmea depicta*. CARLTON (1976) and LINDBERG (1976) both considered "*Notoacmea gabatella*" in papers treating the marine plant limpets of the northeastern Pacific and it was this work that sparked our interest in this species.

SYSTEMATICS

Notoacmea depicta (Hinds, 1842)

- Patelloida depicta* HINDS, 1842: 82; plt. 6, fig. 4; - HINDS, 1845: 53 - KEEN, 1966: 268
- Nacella depicta* (Hinds). CARPENTER, 1857: 318 - CARPENTER, 1864: 650
- Acmaea (Collisella) depicta* (Hinds). DALL, 1871: 254 - DALL, 1921: 170 - OLDROYD, 1927: 759 - ABBOTT, 1954: 104 - ABBOTT, 1974: 32; fig. 162
- Acmaea depicta* (Hinds). PILSBRY, 1891: 19; plt. 6, fig. 40 - ARNOLD, 1903: 317 - GRANT & GALE, 1931: 812 - GRANT, 1933: 59 - KEEN, 1937: 28 - SMITH & GORDON, 1948: 199
- Acmaea (Acmaea) depicta* (Hinds). GRANT, 1937: 75; figs. 293, 294, 316, 317, 332, 333 - BURCH, 1946: 7 - FRITCHMAN, 1961: 58
- Collisella (Notoacmea) depicta* (Hinds). McLEAN, 1966: 112; plt. 3, figs. 20, 21
- Notoacmea depicta* (Hinds). McLEAN, 1969: 19; fig. 6.4 - McLEAN, 1978: 19; fig. 6.4 - CARLTON, 1976: 22 - LINDBERG, 1976: 26
- Acmaea depicta* var. PILSBRY, 1891: 20, 174; plt. 6, fig. 41
- "*Acmaea*" *gabatella* BERRY, 1960: 118 - WILSON & KENNEDY, 1967: 245
- Collisella (Notoacmea) gabatella* (Berry). McLEAN, 1966: 124; plt. 3, figs. 4, 5
- Notoacmea gabatella* (Berry). CARLTON, 1976: 22 - LINDBERG, 1976: 26

Diagnosis: There are 2 *situs* forms of this species, a *Zostera* form and an oval form. A diagnosis for each follows: *Zostera* form (Figure 1) - Shell thin, small (less than 15 mm in length); profile medium; apex positioned in anterior third of shell, anteriorly directed. Anterior slope straight to slightly concave; posterior and lateral slopes convex. Aperture laterally compressed, elongate.

Sculpture of concentric growth lines. Color yellow-white to yellow-brown with darker red-brown chevron markings that radiate outward from the apex and midline of the shell; interior margin slightly darkened, intermediate area lighter. Myostracum vague; central area yellow; anterior slope darkly stained with brown. Shell diaphanous; exterior markings clearly visible through shell.

Oval form (Figure 2) - Shell thin, small (less than 10 mm in length); profile low; apex positioned in anterior third of shell, anteriorly directed, strongly protruding from anterior slope. Anterior slope straight to slightly concave; posterior and lateral slopes distinctly convex. Aperture ovoid, slightly narrowed anteriorly. Sculpture of concentric growth lines. Color yellow-brown with darker red-brown chevron markings that radiate outward from the apex and midline of the shell; interior margin slightly darkened, intermediate area lighter. Myostracum vague; central area with yellow cast. Shell diaphanous; exterior markings clearly visible through shell.

Radula (Figures 3 and 4): First lateral teeth closely set on anterior edge of ventral plates, slightly overlapping anterior ventral plates. Medial edges of first lateral teeth convex, lateral edges sigmoidal; cusps pointed. Second and third lateral teeth positioned obliquely across ventral plates. Second and third lateral teeth twice as broad as first lateral teeth. Medial edges of second lateral teeth slightly convex; cutting edges straight; lateral edge concave, forming small laterally directed cusp. Medial edges of third lateral teeth strongly convex, lateral edge also convex; cutting edge straight; cusp gently rounded. Marginal teeth lacking. Ventral plates squarish with strong anterior process. Ventral plates strongly sutured in vicinity of anterior process and along lateral edge. Small posterior process at medial edge of ribbon units.

Remarks: Although both forms are similar in size, sculpture, and color patterns, the *Zostera* form is laterally compressed, having an elongate aperture and parallel lateral margins that conform in width to its host plant, the eelgrass *Zostera marina*, whereas the oval form has a broadly oval aperture and shows no trace of lateral compression. The oval form is proportionately lower than the *Zostera* form and lacks the dark brown anterior slope stain found in the *Zostera* form. In some fossil specimens of the oval form a dark interior stain is present, but it is posterior to the apex rather than anterior, as it is in the *Zostera* form. McLEAN (1966) pointed out that larger fossil oval forms show a tendency to have raised lateral margins, a character also present in some modern oval specimens, but not found in the *Zostera* form. The radulae of oval and *Zostera* forms show no significant differences

and are well within the range of intraspecific variation seen in other species that have several *situs* forms (e. g., *Collisella ochracea*; *C. pelta*; *C. triangularis*; *Patelloida pustulata*). The only radular differences are in the cusps of the second lateral teeth and the lengths of the ribbon segments. In the *Zostera* form the second lateral tooth cusp is distinctly pointed; in the oval form it is rounded. Also, in the *Zostera* form the ribbon segments are compressed, in the oval form they appear typical of the genus. The remaining radular teeth profiles, arrangement of the teeth, and basal plate morphologies are identical in both forms. Because of the rarity of modern specimens of the oval form, the entire radula was not prepared. Instead, the radula was cut in half and one section preserved with the rehydrated tissues. The shell, tissue, and radula are deposited in the SDMNH alcoholic collection No. 48479.

Notoacmea lepisma (Berry, 1940), an extinct middle Pleistocene species from San Pedro, California, has the same shell markings as *N. depicta*, first noted by McLEAN (1966). *Notoacmea lepisma*, like *N. depicta* is laterally compressed, with parallel lateral margins. However, the profile is distinctly lower and the apex more anterior than in *N. depicta*. According to McLEAN (*op. cit.*) *N. lepisma* is intermediate in shell morphology between *N. depicta* and "*Notoacmea gabatella*." The range of variability of each "species" does not overlap, nor are there any intermediates. My own observations confirm this. If *N. depicta* and "*N. gabatella*" represent extremes of the same species, as I suspect, then *N. lepisma* is also probably a form of *N. depicta*. However, synonymizing *N. lepisma* with *N. depicta* will depend on the results of a morphometric study using coordinate transformation (LINDBERG, in preparation).

Recent Distribution: *Zostera* form – California: Monterey County, Monterey (36°36'N) (ANSP 39142; MCZ unnumbered lot; UCMP 2395); and Santa Barbara County, Mugu Lagoon (34°06'N) (SDMNH 41434) to Mexico: Baja California, Cabo San Lucas (23°N) (CA

SG 17663A). Oval form – California: Los Angeles County, San Pedro (33°45'N) (SU 5478) to Orange County, Laguna Beach (33°33'N) (SDMNH 48479); and San Diego County, San Diego (32°40'N) (USNM 326554). The specimen lots of the *Zostera* form from Monterey, California, were all collected in the nineteenth century, and represent 3 different collectors and dates, evidence that suggests that these are valid records and not mixed specimen lots nor have erroneous locality data. Warm water years in northern California (1853 to 1860) (HUBBS, 1948) may have allowed for the establishment of *Notoacmea depicta* in Monterey Bay in the second half of the nineteenth century. It has not been reported since (*cf.* SMITH & GORDON, 1948).

Fossil Distribution: (Pleistocene) *Zostera* form – California: Los Angeles County, San Pedro, Lomita Marl, (BURCH, 1946), San Pedro Sand (LACMIP Loc. 332); Palos Verdes, Palos Verdes Sand (ARNOLD, 1903); Orange County, Costa Mesa, Terrace cover and Palos Verdes Sand (?) (KANAKOFF & EMERSON, 1959); San Diego County, La Jolla (BURCH, 1946); Mexico: Baja California, La Playa (BURCH, 1946); Ensenada (BURCH, 1946). – Oval form – California: Los Angeles County, San Pedro, San Pedro Sand (LACMIP Loc. 332).

Ecology: The *Zostera* form occurs on the blades of the eelgrass *Zostera marina* (CARLTON, 1976), not on the surfgrass *Phyllospadix* species as reported by McLEAN (1966). *Zostera marina* occurs discontinuously throughout the boreal northern hemisphere from the Seas of Okhotsk and Japan to the Baltic and Mediterranean, and is restricted to shallow water, soft bottom habitats (*i. e.*, lagoons and estuaries) (SETCHELL, 1935).

The oval form of *Notoacmea depicta* occurs on the outer coast (Table 1). Living specimens have been dredged at a depth of 18 m off Reef Point, and at Laguna Beach. The San Pedro specimens were collected from "kelp leaves, stems," possibly *Macrocystis pyrifera* (Linnaeus)

Explanation of Figures 1 and 2

Notoacmea depicta (Hinds, 1842)

Figure 1: *Zostera* form (CASG No. 32762) Shell length - 10.8 mm

Figure 2: Oval form (SU No. 5478)

Shell length - 7.65 mm

Figure 3

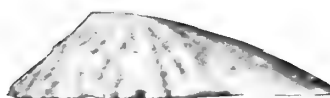
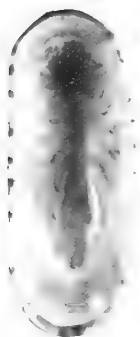
Notoacmea depicta (Hinds, 1842)

Radular ribbon segment of *Zostera* form (CASG No. 49207)

Figure 4

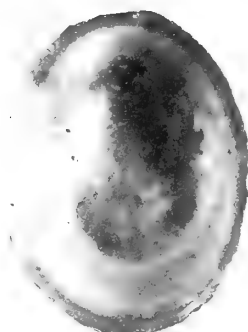
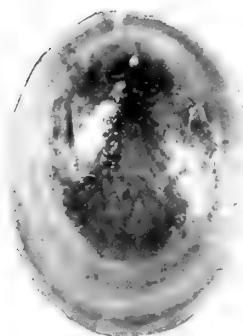
Notoacmea depicta (Hinds, 1842)

Radular ribbon segment of oval form (SDMNH No. 48479)



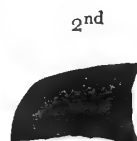
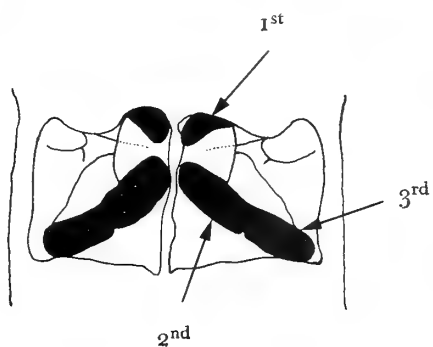
Zostera form

Figure 1



Oval form

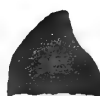
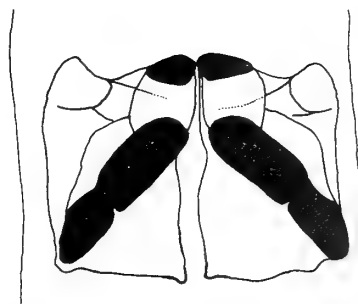
Figure 2



Lateral Teeth Profiles

Zostera form

Figure 3



Oval form

Figure 4

Table 1

Records of Oval forms of *Notoacmea depicta*

Locality (Collector)	Habitat	Authority. Depository (No. of specimens)
CALIFORNIA: Orange County, off Reef Point (A.M. Strong)	Dredged 18 m	BERRY, 1960. SDMNH 50945. Holotype (Type No. 1301) and Paratype (Type No. 1302) of " <i>Acmaea</i> " <i>gabarella</i>
CALIFORNIA: Orange County, off Laguna Beach (A.M. Strong)	Dredged	SDMNH 48479 (5 specimens); (Type Nos. 1303-1307) by WILSON & KENNEDY (1967)
CALIFORNIA: Los Angeles County, San Pedro (Unknown)	kelp leaves, stems	McLEAN, 1966. SU 5478 (2 specimens)
CALIFORNIA: Los Angeles County, San Pedro (Reimer and Kanakoff)	Pleistocene	McLEAN, 1966. LACMIP loc. 332 (approximately 100 specimens)
CALIFORNIA: San Diego County, San Diego, Ballast Point [east side of Point Loma] (Brannan)	?	USNM 32547 (1 specimen)
CALIFORNIA: San Diego County, San Diego (H. Hemphill)	?	PILSBRY, 1891. USNM 32654 (1 specimen)

Agardh, 1830, or any of several other large brown algae. In view of the vast amount of research on *M. pyrifera* that has taken place in southern California, it seems unlikely that the limpet would have been overlooked. No habitat data are available for the San Diego specimens. In view of the cool water fauna of the San Pedro Sand in San Pedro (LACMIP Loc. 332; see below) it is possible that the oval form could occur north of San Pedro today. However, kelp forest studies by McLEAN (1962) and PEARSE & LOWRY (1974) have not reported the form in the Monterey Bay area.

Paleoecology: Although modern specimens of the oval form of *Notoacmea depicta* are few, over 100 specimens are known from a locality (LACMIP Loc. 332) in the San Pedro Sand of San Pedro, Los Angeles County, California. The exposure was a cut bank in the 600 block of Miraflores Street which has subsequently been covered by the southern extension of the Harbor Freeway into San Pedro. Unfortunately, no field notes are available on this locality that might describe the stratigraphic section or indicate whether one or several shell horizons were collected. It is not now possible to tell if the bathymetric discrepancies indicated by the molluscan fauna at this locality are a product of downslope reworking of detrital shells or a result of collecting through a stratigraphic section in which shoaling might have been involved.

The only published discussion on the paleoecology of this locality is that by FITCH (1967). He reported 38 species of fish, mainly as otoliths. Several additional fish taxa are also listed by LANGENWATER (*in* KENNEDY, 1975).

Fitch's study indicated a "cold water" fauna similar to one that would occur off central California today. Analysis of the bathymetric ranges for each species (bathymetric data from MILLER & LEA, 1972) gives the following results. Seventy-nine % (30 species) occur in depths less than 15 m, 87% (33 species) occur between 15 m and 50 m depths, and 90% (35 species) occur between 50 m and 70 m depths. Below 70 m only 72% (27 species) remain. This suggests a depositional depth between 30 m and 70 m, the lesser depth suggested by the upper limits of several deep water species. The habitats represented by the fish are diverse and include epipelagic (sharks), sand or mud bottom (flounders and rays), off shore (herring and anchovy), and rocky bottom (rock fish, wrasse, and sculpins).

A preliminary list of mollusks from LACMIP Loc. 332 (G. L. Kennedy, *in litt.*, 1978) was used to infer the bathymetric, habitat, and thermal conditions of the molluscan fauna. The fauna, taken in aggregate, indicates depth ranges from intertidal to over 500 m. However, both intertidal and deep water species are few in number and are represented by few specimens. The major part of the mollusks occur today at depths between 15 m and 70 m. WOODRING *et al.* (1946), using molluscan data from other localities, suggested that the San Pedro Sand represented shallow water deposits at some localities and moderate depths (50 m to 90 m) elsewhere. VALENTINE (1961) considered the San Pedro Sand to represent depths between 18 m and 90 m. LACMIP Loc. 332 appears to contain both shallow water and moderate depth species.

The molluscan component at LACMIP Loc. 332 is not distinctly cold or warm water. Instead, it includes several cryophilic (*i. e.*, northern) and thermophilic (*i. e.*, southern) members. The majority of the species present have modern distributions that include San Pedro. FITCH (1967), like WOODRING *et al.* (1946), felt the fauna indicated a cooler water environment. VALENTINE (1961) stated that the faunas representing depths greater than 27 m suggested cooler waters than those in the area today.

Habitat data are by far the most confusing. Several biotopes are represented in the molluscan component including shallow water embayment, protected rocky coast, kelp forest, and both sand and mud bottoms. Of the 179 species (Kennedy, *in litt.*, 1978) from LACMIP Loc. 332, the oval form of *Notoacmea depicta* ranks 23rd in abundance (approximately 100 specimens). The *Zostera* form of *N. depicta* is represented by only 2 specimens. Other abundant species and their habitats are given in Table 2. The paleoecological setting of LACMIP Loc. 332 suggests several possible habitats for the oval form of *N. depicta*, ranging from shallow embayment to rocky subtidal. However, the modern occurrences clearly support the latter, particularly a kelp forest habitat.

WEHMILLER *et al.* (1977) have estimated the age of the San Pedro Sand, based on racemization of leucine in *Protothaca* shells from LACMIP Loc. 332, at 320 000 to 410 000 \pm 80 000 BP, thus placing it within the middle Pleistocene as currently defined.

SUMMARY

Notoacmea gabatella (Berry) is synonymized with *N. depicta* (Hinds). This action is based on the identical radular morphologies found in both "species." *Notoacmea depicta* is considered to be a polytypic species with 2 forms – a laterally compressed form on the eel grass *Zostera marina*, and an oval form thought to occur on or near large brown algae. The oval form is extremely rare in the Recent fauna, being represented by fewer than 10 specimens. In the middle Pleistocene of San Pedro, California, it is represented by more than 100 specimens at a single locality (LACMIP Loc. 332). The paleoecology of LACMIP Loc. 332 is consistent with the Recent habitat and suggests depositional depths between 30 m and 70 m.

Table 2

Abundant (>500 specimens) Mollusks from LACMIP loc. 332

Species	No. of specimens	Depth	Habitat	Authority
Gastropoda				
<i>Lirularia optabilis</i> (Carpenter, 1864)	968 \pm	Known only from Pleistocene assemblages		McLEAN, 1964
<i>Turritella cooperi</i> Carpenter, 1864	1500 \pm	>20 m	sand, mud bottoms	McLEAN, 1978
<i>Bititium armillatum</i> Carpenter, 1864	1309 \pm	Probably restricted to Pleistocene		WOODRING <i>et al.</i> , 1946; teste McLEAN, 1979
<i>Bititium munitum</i> (Carpenter, 1864)	1850 \pm	24 m	fine sand, shale fragments	SMITH & GORDON, 1948
<i>Bititium rugatum</i> Carpenter, 1864	>1000	60-80 m	?	CARPENTER, 1866
<i>Mitrella tuberosa</i> (Carpenter, 1864)	2070 \pm	subtidal	not uncommon in gravel under kelp	McLEAN, 1978
<i>Alia carinata</i> (Hinds, 1844)	> 500	low intertidal to subtidal	near surf grass and algae	McLEAN, 1978
Bivalvia				
<i>Acila castrensis</i> (Hinds, 1843)	600 \pm	16-500 m	sandy mud	SCHENCK, 1936; ABBOTT, 1974
<i>Mysella aleutica</i> (Dall, 1899)	1500 \pm	20-130 m	fine sand, shale fragments	ABBOTT, 1974; SMITH & GORDON, 1948
<i>Luciniscia nuttalli</i> (Conrad, 1837)	many hundreds	low intertidal to subtidal	sand flats—off shore	McLEAN, 1978
<i>Transennella tantilla</i> (Gould, 1853)	>2000	low intertidal to 36 m	sand, sandy mud semi-protected bays and off shore	HERTLEIN & GRANT, 1972; COAN & CARLTON, 1974

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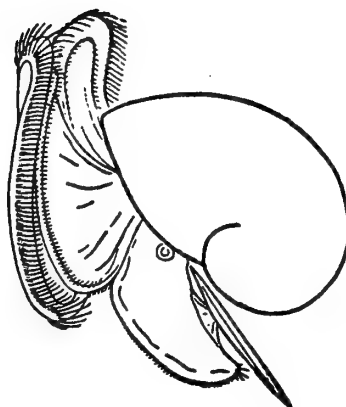
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Reinstatement of Two Species of *Murexiella*

(Gastropoda : Muricidae)

from the Tropical Eastern Pacific

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(1 Plate; 1 Text figure)

IN THEIR RECENTLY PUBLISHED book on the Muricidae, RADWIN & D'ATTILIO (1976) synonymized *Murexiella keenae* and *M. laurae*, both described by VOKES, 1970, with *M. humilis* (Broderip, 1833). Specimens collected by dredging along the west Mexican coast over the past 24 years suggested that the 3 closely related species recognized by Vokes are valid.

In order to base my conclusions on as many specimens as possible, material from 7 major collections was examined. The material was identified as follows: *Murexiella humilis*, 23 lots, 60 specimens; *M. keenae*, 15 lots, 52 specimens; *M. laurae*, 8 lots, 45 specimens.

The following characteristics were considered significant: general outline of the shell, form of the nucleus, number of varices, form of the spiral cords, microscopic spiral threads, shape of spines on the shoulder and canal, number of spiral cords and spines on the canal.

No difficulty was encountered in separating the material, including several mixed lots, into 3 distinct and homogeneous groups. Immature shells (under 4 mm) of the 3 species, which more nearly resemble each other, were also easily separated. The 3 groups were compared with the holotypes for *Murexiella keenae* and *M. laurae* and with the original description and figure for *M. humilis*. The geographic distribution of each species is shown in Figure 7.

Specimens from Manzanillo, Colima, Mexico, were selected for comparison. They included a significant number of each species and came from the same area of several square kilometers. All 3 species were dredged from the same substrate of coarse gravel and small rocks in 20 - 30 meters off a rocky headland.

Murexiella humilis (Broderip, 1833)

(Figures 1, 4)

Murex humilis Broderip, 1833; SOWERBY, 1834: plt. 65, figs. 46, 47

Murex norrisii REEVE, August 1845: plt. 28, sp. 129A-B

Murexiella humilis. VOKES, 1970: plt. 50, figs. 1 - 3; KEEN, 1971: fig. 988; RADWIN & D'ATTILIO, 1976: plt. 25, fig. 4

Murex humilis Broderip, 1833, was described with Santa Elena, Ecuador, as type locality. The species was first figured by SOWERBY (1834). The description and figure are of a shell with a globose body whorl, a moderately elevated spire of about 5 whorls, and a long, nearly straight canal. Varices are fimbriated along the leading edges and are intersected by spiral cords. The intersections give rise to spines that terminate sharply and are spirally recurved. Below the body whorl, on the upper part of the canal, is a wide band where the axial and spiral sculpture is greatly subdued. Anteriorly on the canal are 3 rows of sharp recurved spines that rise from the terminations of spiral cords at the leading edges of obsolete canals.

Based on the large number of specimens examined, further details may be added. The nucleus is conical, of 3 globose whorls, the first small, the other 2 increasing regularly. The tip is immersed. The entire nucleus is covered with microscopic granules. The first postnuclear whorl has 8 low axial ribs that extend over the third nuclear whorl and are attached to it for the lower $\frac{1}{3}$ of its height.

The varices are formed by the terminations of successive growth stages. In mature specimens, the thin outer layer of each growth stage is reinforced with successive layers of shell material deposited on the inner surface. The layers are slightly separated along the terminal edge.

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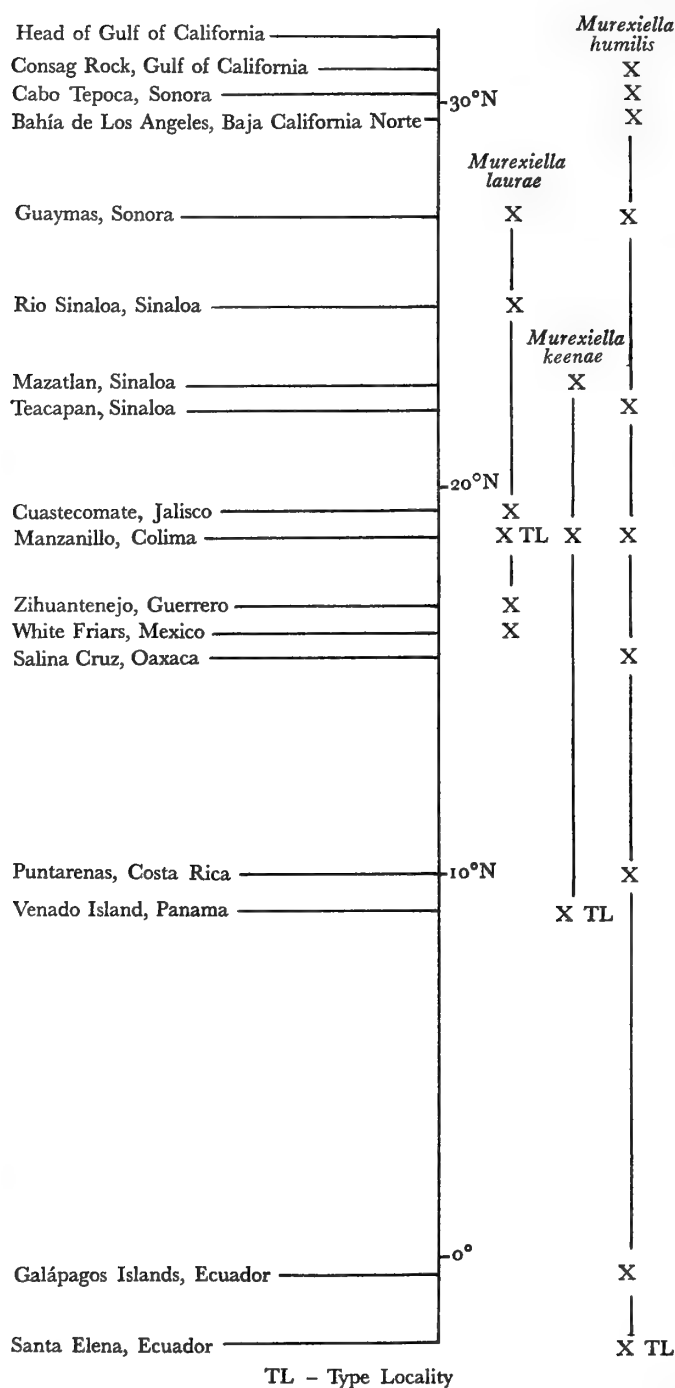


Figure 7

Each growth stage is begun below the last layer of the preceding one. Thus, the leading edge of each varix is exposed as an expanded frilly cross section of the shell wall. Although all specimens examined began postnuclear growth with 8 varices per whorl, some increased the number with growth and some decreased. The range for the number of varices on the adult body whorl was 6 to 9, with 56% of the specimens having 8.

There are 5 major cords on the body whorl, 2 on the spire, and 3 anteriorly on the canal. Each major cord is marked by 9 to 14 small grooves and resembles a bundle of fine threads. At the termination, these smaller threads broaden axially and end successively from the outside in toward the heaviest central thread. The entire spine is recurved spirally as much as 180° and terminates sharply. In some cases, a secondary thread separates and recurves to form a second smaller spine. Between the heaviest cord at the shoulder and the suture is a minor cord with minor spines.

The 3 rows of spines on the anterior one-half of the siphonal canal occurred on 81% of the specimens. The other 19% had only 2 rows. In this case, a third obsolete row was apparent on some specimens. On others, a third row was present on earlier growth stages but became obsolete before the final varix. Three rows of spines on the anterior part of the canal seems to be normal for this species.

Murex norrisii Reeve, 1845, was compared in the original description with *M. humilis*. The only significant difference noted was several rows of very small, sharp spines in the nearly smooth region on the canal anterior to the aperture. Reeve's illustration shows these. All specimens of *M. humilis* showed 3 to 5 small cords in this region terminating as small straight spines. Most of these were broken off; but some of them were intact and were as much as 2 mm in length. Comparable spines were also

Explanation of Figures 1 to 6

Figure 1: *Murexiella humilis* (Broderip, 1833)

Figure 2: *Murexiella humilis* (Broderip, 1833)

Figure 3: *Murexiella keenae* Vokes, 1970

Figure 4: *Murexiella keenae* Vokes, 1970

Figure 5: *Murexiella laurae* Vokes, 1970

Figure 6: *Murexiella laurae* Vokes, 1970

All 3 specimens were dredged in 20 to 30m off Punta Juluapan, Colima, Mexico
all figures X5



Figure 1



Figure 3



Figure 5



Figure 2



Figure 4



Figure 6

noted on the other 2 species. This is probably a characteristic of the "*humilis*" group in the sense it is used by VOKES (1970).

Murexiella keenae Vokes, 1970

(Figures 2, 5)

Maxwellia (?) *humilis*. KEEN, 1958: 354; fig. 342

Murexiella keenae VOKES, 1970: 328; plt. 50, figs. 8-10;

KEEN, 1971: 519; fig. 989

Murexiella humilis. RADWIN & D'ATTILIO, 1976: 157; plt. 25, fig. 5

The species was very adequately described and figured. The holotype (LACMNH 1259) is more globose than other specimens collected recently from the same area. Shells from the northern part of the range tend to be still more slender and less fimbriated; but the distinguishing characteristics are strongly apparent throughout the range.

The nucleus resembles that of *Murexiella humilis*, except that the third whorl does not increase regularly but is much more inflated. Also, the axial ribs of the first post-nuclear whorl extend completely across the third nuclear whorl.

Postnuclear growth begins with 8 varices per whorl but decreases to 6 in the fully adult stage. The leading edge of each varix is heavier, more fimbriated, and more recurved than those of the preceding species.

The spines at the terminations of the spiral cords are short and axially triangular, recurved, and flexing toward the apex. The spines on the shoulder are subdued and may be only a slight prominence on the thin lamella-like varices. The rows of spines anteriorly on the canal are reduced to 2. The minor cords, which make up the major cords, fan out axially at their terminations to form spatulate recurved spines that do not terminate sharply.

The major and minor cords are somewhat like those of *Murexiella humilis*; but the entire surface is also covered with microscopically fine spiral striations and, in some cases, growth lamellae.

Murexiella laurae Vokes, 1970

(Figures 3, 6)

Murexiella laurae VOKES, 1970: 328; plt. 50, figs. 4, 5; KEEN, 1971: 519; fig. 991

Murexiella humilis. RADWIN & D'ATTILIO, 1976: 157; plt. 25, fig. 3

This species was also well described. It is much different from *Murexiella humilis*. The nucleus is lower and more turbinate. The axial varices of the first postnuclear whorl extend completely across the third nuclear whorl.

Adult growth begins with 8 varices per whorl but decreases to 6 by the fourth whorl and to 4 on the fully adult shell (only 3 on several specimens). The varices are progressively thicker and more reflected with growth. On the shoulder, they appear as reflected lamellae, fimbriated on the leading edge and with a spine in the middle.

The spiral cords on the body whorl of the juvenile shell are very broad, nearly flat surfaced, and with narrow interspaces. The cords are high and irregularly nodose from incremental growth. On the adult whorl, these cords are reduced to low, smoothly rounded ridges especially prominent toward the terminal edge of the varix. The cords become stronger here and, as they join the reflected edge, give rise to low, broadly triangular spines, which are sharply recurved. The spine at the shoulder is the heaviest, recurved and flexed toward the apex.

The canal is nearly closed. For the first one-half of its length, it is at an angle of 30° to the left of the axis. Then, it abruptly flexes to the right and is parallel to the axis for the second one-half. Only the tip is reflected dorsally. The first one-half of the dorsum of the canal is nearly smooth, showing several weak cords between low varices. Anteriorly are 2 rows of spines formed by weak spiral cords. The spines are spatulate and end in 3 or more of the lesser threads that make up each of the major cords. The entire shell is covered with microscopically fine spiral striations.

The holotype of *Murexiella laurae* (LACMNH 1260) is not fully adult. Only the last 2 growth stages, ending in the typically heavy varices, are adult ("growth stage" is defined here as the growth of the shell from one varix to the next succeeding one). Unfortunately, this does not show in the original illustration (VOKES, 1970), in which the sculpture at the left of the aperture is typical of the juvenile form.

DISCUSSION

Murexiella humilis occurs from Santa Elena, Ecuador, northward nearly to the head of the Gulf of California. It has not been reported in the Gulf of Panama. The

members of this species prefer silty bottom among rocks in 20 - 30 m.

Murexiella keenae is uncommon intertidally among rocks at Venado Island, Panama. On the west Mexican coast, it has been dredged as far north as Mazatlán, Sinaloa, in 20 - 30 m on small rock and gravel bottom off rocky headlands.

Murexiella laurae has been reported from White Friars, Mexico, to Guaymas, Sonora. It has been dredged in 20 - 30 m on small rock and gravel bottom off rocky headlands.

It is to be expected that more intensive searching will extend the ranges of the last 2 species northward and southward, perhaps to more nearly correspond to that of *Murexiella humilis*.

ACKNOWLEDGMENTS

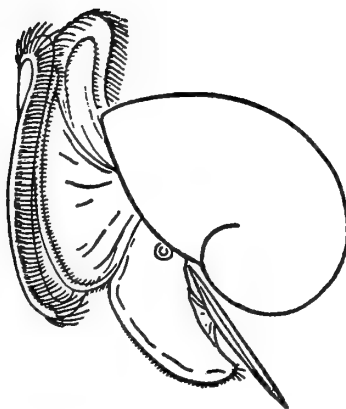
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Larval and Early Benthic Stages of *Brachidontes granulata*

(Bivalvia : Mytilidae)

BY

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(2 Plates)

INTRODUCTION

Brachidontes granulata (Hanley, 1843) is a mytilid distributed from Lobos, Perú (6°S) to Isla Chiloé and Seno Reloncaví, Chile (43°S) (SOOT-RYEN, 1959). It may be found attached to undersides of rocks in the lower intertidal zone (MARINCOVICH, 1973), and forming small groups under the mats of various algae in intertidal pools in the rocky areas of Central Chile (STUARDO, 1960). In Montemar, Valparaíso (33°S), *B. granulata* is more abundant in the semisheltered zone. Other mytilid species that occur in the same area are: *Perumytilus purpuratus* (Lamarck, 1819), *Semimytilus algosus* (Gould, 1850) and *Aulacomya ater* (Molina, 1782).

Brachidontes granulata has been included in the subgenus or genus *Hormomya* together with *Mytilus adamsianus* Dunker, 1857 (SOOT-RYEN, 1955). However, KEEN (1971), adopting a conservative classification recognizes only the genus *Brachidontes*. This matter needs clarification in order to properly evaluate the differences found in the larval stages of the species included in *Brachidontes sensu lato*.

The following contributions have been made in relation to the larvae of bivalve species from the Chilean coast: RANSON (1960), HOLLIS & MILLAR (1963), PADILLA & ORREGO (1967), and SOLÍS (1967) on *Ostrea chilensis*; WALNE (1974) on *Choromytilus chorus* (misspelled as *C. choro*); PADILLA (1973) on *Mytilus edulis chilensis* and SOLÍS, SÁNCHEZ & NAVARETTE (1976) on bivalve larvae from the Estero de Castro. Only RANSON (*op. cit.*) and SOLÍS, SÁNCHEZ & NAVARETTE (*op. cit.*) described the morphology of the larval shell.

No descriptions of larvae of either *Hormomya* or *Brachidontes* are known to us, except the paper of CHANLEY (1970) on *B. recurvus* from the western North Atlantic Ocean. YOSHIDA (1937) described the larvae and early

juveniles of *B. senhausi* (Reeve), but according to KURODA *et al.* (1971) this species belongs to the genus *Musculus*.

The purpose of this paper is to describe the larvae and early benthic stages of *Brachidontes granulata* so that they may be identified in planktonic and benthic samples. This information should prove especially useful in areas where other species of Mytilidae are cultivated for commercial purposes.

MATERIALS AND METHODS

Sexually mature adult mussels were collected at the intertidal zone near Montemar. In the laboratory all specimens were washed and placed in plastic dishes with filtered sea water (0.8 μ m membrane filter) and held in an incubator at 6°C for 12 hours. Thereafter, they were changed to filtered sea water at 16°C where they usually began to spawn about 5 hours later.

Unfertilized eggs were poured through a set of nylon screens with mesh openings from 150 to 55 μ m to remove debris. They were immediately placed in a finger bowl with filtered sea water, where some drops of sperm suspension were added. Fertilized eggs were kept without movement for 30 minutes, being transferred to a culture vessel with 2 L of filtered sea water at laboratory temperature (12 - 16°C). Three days later, when the end of the prodissococonch I was reached, air and a food mixture of *Tetraselmis* and *Nannochloris* were added; the concentration of algal food was not controlled. During the experiment the larvae were washed, sea water was changed and new food was added every 2 days. As the larvae of *Brachidontes granulata* were only cultured up to the early dissoconch stage, the description of the early benthic stages was made from recently settled individuals collected in the same area where adults came from.

Cleaned valves were examined, measured and photographed, using a Leitz Ortholux microscope with an Orthomat camera.

The terms prodissoconch I (= prod. I), prodissoconch II (= prod. II) and dissoconch follow WERNER (1939) and REES (1950). The terms veliger and pediveliger are defined in CHANLEY & ANDREWS (1971).

RESULTS

Brachidontes granulata is a dioecious species. Spawning eggs were brown in color with a mean diameter of 66.3 μm and a size range of 63 to 73 μm ; sample size: $n=100$.

The prod. I was colorless, transparent, and the measurements in μm were: mean length 117, s. d. 5.3, range 105 - 126; mean height 69.7, s. d. 3.9, range 63 - 73.5; $n=100$.

The evidence of the prod. II development was a yellow edge in the shell material surrounding the prod. I. Simultaneously with the initial growth of the prod. II appeared a taxodont dentition, bearing an indeterminate number of small central teeth and 2 more prominent ones at the ends of the hinge line. As the larval shell was growing, the 2 largest teeth increased in size, and in number to 6 or 7, forming the curved end of the provinculum in the pediveliger stage. The umbo appeared at about 150 μm larval length as the result of the growing towards the central side of the largest provincular teeth. The dorsal side of the hinge line remained relatively flat, forming a broadly rounded umbo.

The eyespots appeared at 160 μm larval length. A notorious ligament slightly displaced towards the posterior side could be seen in larvae 180 μm in length. As larvae attained a length of 190 μm , the foot was evident between the valves and became functional at 200 μm length. The velum disappeared at 215 μm larval length.

At the pediveliger stage the larval shell of *Brachidontes granulata* could be characterized as follows: yellow prodissoconch, anterior margin curved, posterior end almost

straight, ventral margin nearly circular, shoulders almost straight, the anterior being longer than the posterior one and not sloping as steeply, umbo broadly rounded and more prominent in width than in height. The mean length in μm of the prod. II was 215, s. d. 5.3, range 200 - 231; $n=100$.

The correlation of the major features of larval development and sizes of *Brachidontes granulata* reared in the laboratory, is summarized in Table 1, and the main characteristics of the larval shell are shown in Figures 1 to 6.

Table 1

Summary of the major features of larval development in *Brachidontes granulata*. Temp. 12-16°C; S.34-35‰

Stage or distinctive feature	Mean size microns	Mean age
Unfertilized egg	66.3	
Trochophore	73.0	20 hours
Prodissoconch I	117.0	3 days
Early umbo	150.0	12 days
Appearance of eyespots	160.0	22 days
Ligament evident	180.0	28 days
Foot	190.0	30 days
Functional foot (pediveliger)	200.0	40 days
Loss of velum	215.0	55 days

The shell of the early juveniles collected from the intertidal zone shows the following characteristics (Figures 7 to 13): The dissoconch is colorless and transparent; this feature serves to easily distinguish the limit of the yellow prod. II. About 290 μm in length (maximal distance parallel to the hinge), the shell shows a conspicuous growth towards the ventero-posterior end. At a length of about 400 μm , the anterior ventral margin of the shell is straight and the umbo is prominent; also the first disso-

Explanation of Figures 1 to 7

Larval and early benthic stages of *Brachidontes granulata*

Figure 1: Internal view of the larval shell, right valve; length 126 μm

Figure 2: Internal view of the larval shell, right valve; length 190 μm

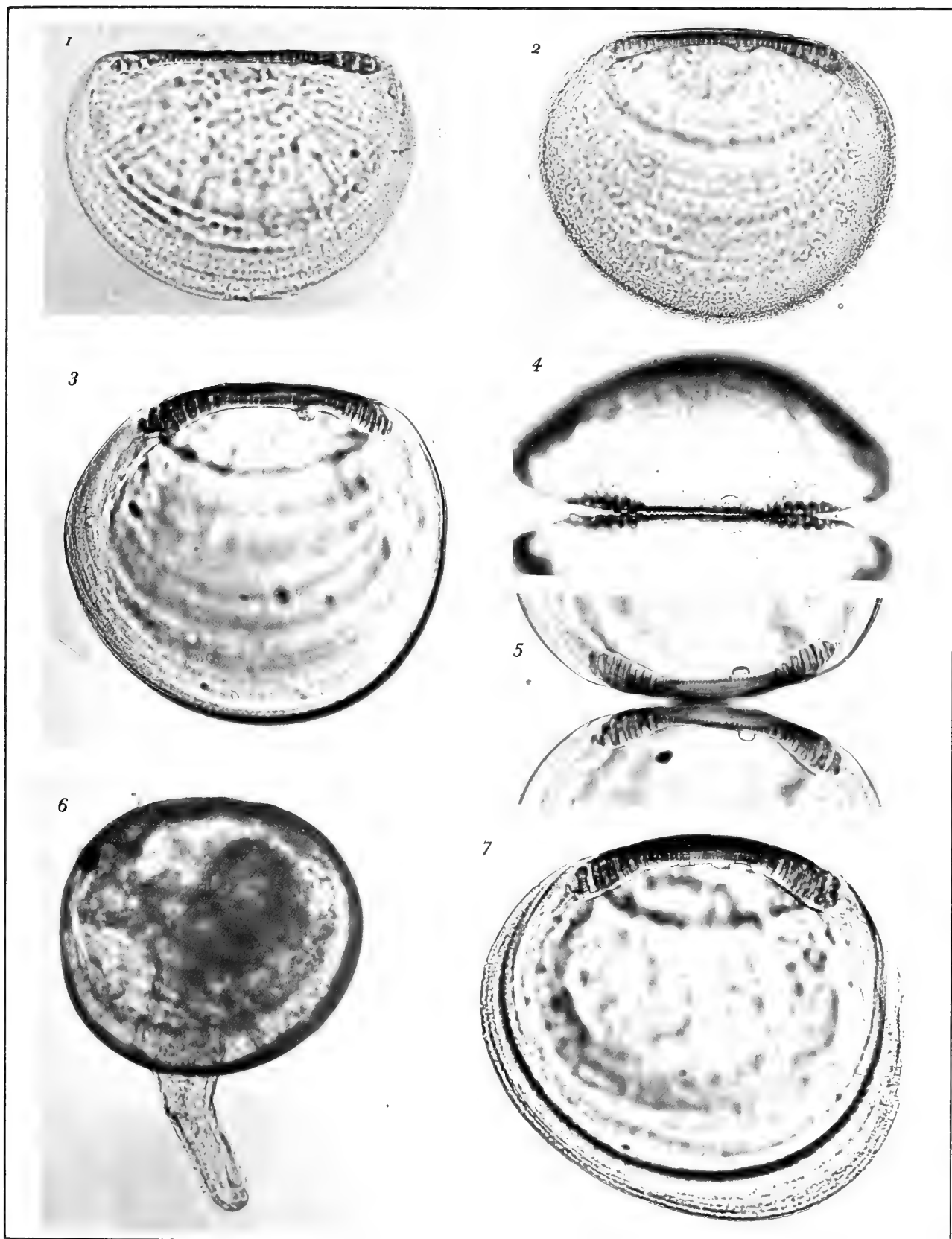
Figure 3: Internal view of the larval shell at the pediveliger stage, right valve; length 210 μm

Figure 4: Hinge structure of the larval shell at the pediveliger stage, dorsal view. Shell length 210 μm

Figure 5: Hinge structure of the larval shell at the pediveliger stage, internal view. Shell length 210 μm

Figure 6: Larva at late pediveliger stage; length 220 μm

Figure 7: Internal view of the right valve at early benthic stage showing the initial dissoconch; length 240 μm



conch teeth (Cox, 1969) develop along the posterodorsal margin some distance beyond the larval hinge. At shell lengths ranging from 450 to 550 μm , a new zone grows in the dissoconch; this new zone is characterized by the presence of radial ribs deeply impressed, a slight sinus in the ventral margin and a white coloration contrasting with the first colorless zone of the dissoconch.

DISCUSSION

Although the main purpose of this work was the description of larval and post-larval stages of *Brachidontes granulata*, the method used allowed us to obtain additional information on the development of the larvae under laboratory conditions.

The common methods to induce spawning of sexually mature bivalves in the laboratory are thermal, chemical and electrical shock, sex products stimulation and stretching the posterior adductor muscle (LOOSANOFF & DAVIS, 1963). The review of the literature reveals the difficulties of inducing bivalves to spawn, and that there is no agreement as to which stimulus is best for each species. The insertion of a small wooden wedge between the shells and stretching of the adductor muscle was unsuccessful in *Brachidontes granulata*. However, rapid cooling and warming of the water always stimulated spawning of abundant eggs and sperm, giving rise to healthy larvae.

From the investigations carried out to date (CARRIKER, 1961; LOOSANOFF & DAVIS, 1963; BAYNE, 1965; LOOSANOFF, DAVIS & CHANLEY, 1966; DESCHWEINITZ & LUTZ, 1976), it is reasonable to infer that in bivalves many features, such as larval shells, eyespots, foot, etc., appearing during the larval stages up to metamorphosis, seem to be primarily dependent on size rather than age, temperature, food, or other environmental factors. This conclusion suggests the validity of correlating the larval dimensions with the shape of the larval shells, as well as the other structures already mentioned, even if the individuals may show small variations in the size at which a given feature appears. This generalization has led us to rear *Brachidontes granulata* with minimal laboratory requirements, regardless of the duration of the larval development.

Cultured larvae reached the pediveliger stage by the 40th day at a mean size of 200 μm in length. Later, the velum gradually degenerated, disappearing by the 55th day. These larvae were kept alive until the end of the experiment for another 18 days, and no attachment was observed during this time; this fact suggests a delay of metamorphosis in *Brachidontes granulata* larvae. Our

results agree with those of BAYNE (1965) on *Mytilus edulis*, mainly in relation to the events that occur during the delay of metamorphosis. This same author emphasizes that the major factor influencing the delay of metamorphosis is the availability of a suitable substrate capable of stimulating the secretion of the byssus gland. Although no experiments on the effects of environmental factors in the metamorphosis were carried out by us, the fact that suitable substrates were not offered to pediveligers, might have been the cause of non-attachment in *B. granulata* larvae.

From the studies of LOOSANOFF (1961), CARRIKER (1961), LOOSANOFF & DAVIS (1963) and BAYNE (1965), we infer that it is difficult to ascertain the precise moment of metamorphosis. It is rather a gradual process, preceded by the pediveliger stage, and ending with the development of a functional byssus gland and the appearance of the dissoconch shell.

Neither functional byssal gland nor growth of the shell were observed during the 33 days after the larvae of *Brachidontes granulata* reached the pediveliger stage, except for a narrow white band of shell that marked the beginning of the dissoconch.

While culturing *Anomia simplex*, LOOSANOFF (1961) observed the disappearance of the velum, retention of a functional foot, and the beginning of the dissoconch without attachment to the substratum. This experience is very similar to ours, except that the shell of *Brachidontes granulata* did not grow appreciably as in *A. simplex*. LOOSANOFF (*op. cit.*) named this phenomenon 'partial metamorphosis without attachment to the substratum.' We do not know if the byssal gland in *B. granulata* could become functional in case that a suitable substrate had been added after the beginning of the dissoconch growth. These "abnormalities" in the metamorphosis process should be further investigated before any feature delimiting the end of metamorphosis can be properly ascertained.

Larvae of *Brachidontes granulata* are typical pelagic mytilid larvae. Compared with those of *B. recurvus* from the coast of Virginia in the North Atlantic (CHANLEY, 1970), the former have a more rounded shell, the large teeth of the provinculum appear at a bigger larval size (126 against 105 μm in *B. recurvus*) and have a distinct ligament. Egg diameter, umbo shape and size at which the eyespots appear are about the same in both species.

A shell area located immediately beyond the prodissoconch and differing conspicuously from the final dissoconch in the early bottom stages of some mytilids, has been described as an "interdissoconch" (JØRGENSEN, 1946; REES, 1950).

OCKELMANN (1965) has pointed out that such inter-dissoconchs also occur in some species of other families besides Mytilidae and Pectinidae, so there may be as many as 4 different stages of shell formation in marine bivalves. On the other hand, CARRIKER (1961) described 2 different zones in the dissoconch of *Mercenaria mercenaria*, calling them dissoconch with primary shell ridges and dissoconch with secondary shell ridges.

These observations agree with ours, since in *Brachidontes granulata* 4 stages in shell formation are also clearly shown. After a yellow prod. II, there is a transparent zone bearing only circular striae, and beyond a white shell with the typical radial striae of the adult (Figures 12, 13).

Summarizing, we confirm for this species that besides prod. I and prod. II, there is a dissoconch structurally divided into 2 different types of shell: the so-called interdissoconch of some authors and the final dissoconch.

SUMMARY

The description of the larvae and early benthic stages of *Brachidontes granulata*, employing cultured larvae under laboratory conditions, and intertidal benthic samples from Valparaíso Bay is presented.

A partial metamorphosis without attachment to substratum of the cultured larvae is discussed. In the pediveliger larvae the velum was lost and a narrow band of dissoconch was formed, but no functional byssal gland was observed.

The dissoconch of *Brachidontes granulata* is structurally divided into 2 different zones. One of these should correspond to the so-called interdissoconch of other authors.

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Explanation of Figures 8 to 13

Early benthic stages of *Brachidontes granulata*

Figure 8: External view of the right valve; length 290 μ m

Figure 9: Internal view of the hinge structure, right valve; shell length 290 μ m

Figure 10: External view of the right valve; length 440 μ m

Figure 11: Hinge structure of the right valve; shell length 440 μ m

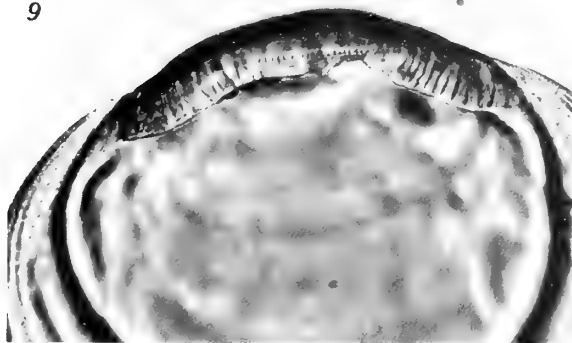
Figure 12: External view of the right valve; length 500 μ m

Figure 13: External view of the right valve; length 590 μ m

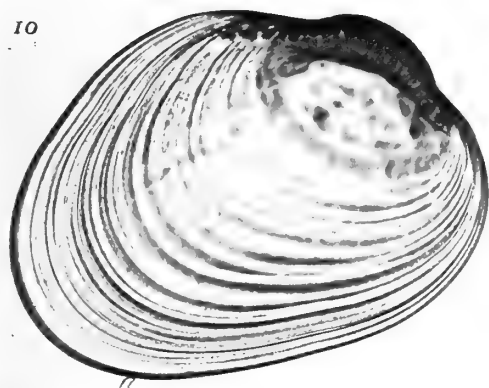
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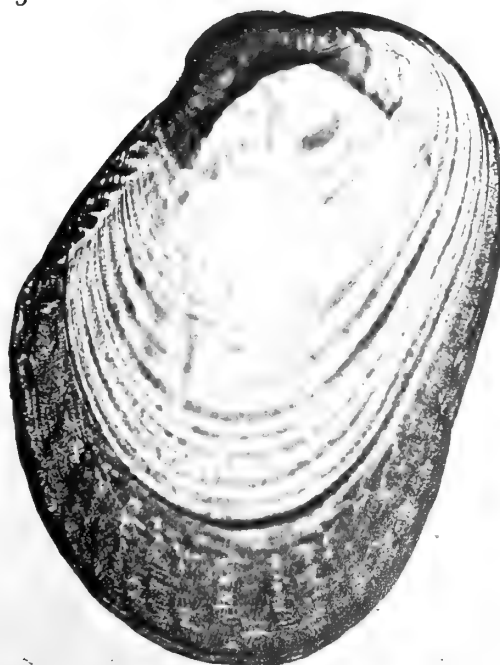
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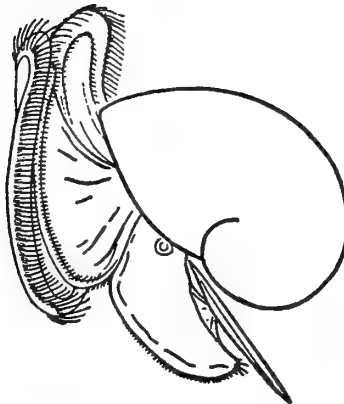
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Deep Water Collections of Opisthobranchs in Central California

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(2 Text figures)

LITTLE IS KNOWN concerning the biology of opisthobranch mollusks in the deep water continental shelf areas of California. A few papers report the depths and locations of particular deepwater species (SMITH & GORDON, 1948; HANNA, 1951; CHIVERS, 1966; MACFARLAND, 1966; BERTSCH, 1969; CARLISLE, 1969; LEE & BROPHY, 1969; McDONALD & NYBAKKEN, 1975). Many more reports are available, however, describing the ecology of those species residing in shallow inshore waters.

This report describes the findings of 6 opisthobranch species from 3 deepwater trawls off Central California. The species, their depths (several representing substantial extensions) and associated food items are discussed.

METHODS

Opisthobranchs were collected in conjunction with normal commercial trawl fishing activities on the vessel *Silver Queen*. The senior author accompanied the fishermen to collect any non-commercial specimens brought up in the trawls. Trawl samples were sorted on board and all invertebrate material was preserved in 10% buffered formalin solution and taken to the laboratory for further examination. In the laboratory, the stomachs were opened and flushed with formalin solution and the contents were examined microscopically for food material, which was then identified to the lowest taxonomic level possible.

Opisthobranchs were found in 3 of 11 trawls, taken 9.6 km off Point Piedras Blancas, California (Figure 1), January 27 to 31, 1978. Trawls ranged in depth from 112 to 360 m, and lasted 3 to 5 hours at a speed of 2 knots.

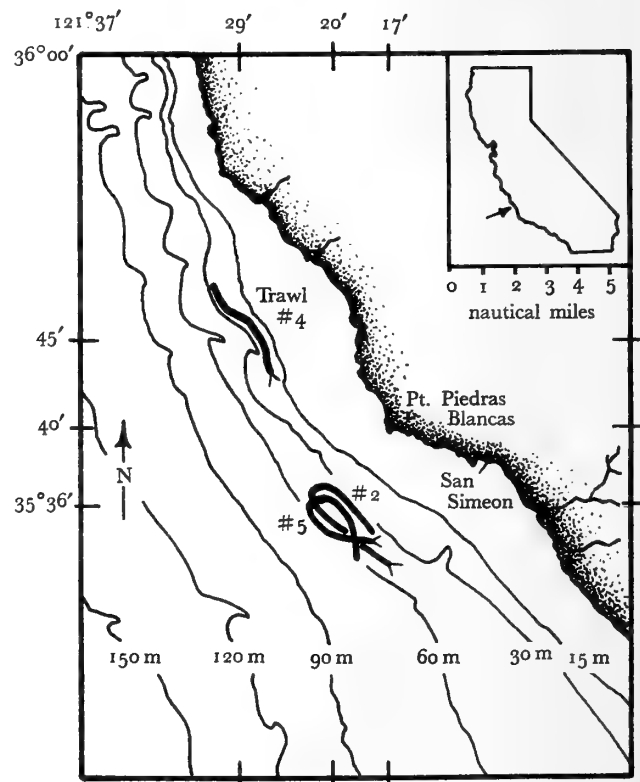
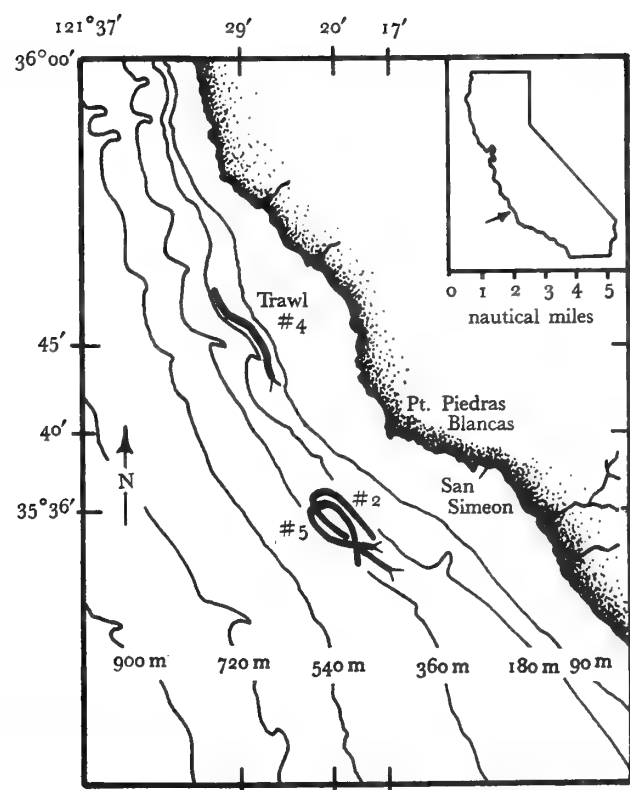


Figure 1

Map of Point Piedras Blancas area showing location of the 3 trawls

The original map submitted with the manuscript showed depth contour lines labeled in "f". As *The Veliger* is strictly metric, the measurements were converted to "m". However, after publication, we were informed that "f" stood for "fathoms", not "feet"; the abbreviation should have been "fm". We present herewith a corrected version of the map with the suggestion that it be pasted over the incorrect map on page 282 of volume 22. Caution: do NOT use rubber cement.



OBSERVATIONS AND DISCUSSION

In spite of the obvious geographical separation of trawl 4 from 2 and 5 (Figure 1), we have chosen to discuss trawl 2 and 4 together as the first collection because of the similarity of species composition and substrate. Trawl 5 is treated separately as a second collection.

Trawl number 2 (Table 1), taken January 27, 1978, occurred at a depth of 236-291 m. Substrate materials sorted from the trawl were mud, sand and boulders. Trawl number 4, although shallower (107-218 m), produced similar bottom materials. The species composition of live material from the 2 trawls was the same (Table 2).

A single specimen of *Pleurobranchaea californica* MacFarland, 1966, was collected in each trawl. They measured 100 and 95 mm (preserved), respectively. Our collections are consistent with CHIVERS (1977) who reported the bathymetric range of the species to be 9 to 369 m and its substrate to be green mud.

Stomach contents analysis of the *Pleurobranchaea* from trawl 2 produced an interesting assemblage of food items which we feel gives an accurate account of this species' benthic foraging existence. The stomach material included 5 specimens of an unidentifiable species of *Aglaja*. The specimens ranged from 6-8 mm in length (preserved). The cephalic shield and mantle were mottled brown in

Table 1

Trawl Location and Substrate Data

Trawl #	Date	Depth (m)	Latitude	Longitude	Substrate
2	Jan. 27, '78	236-291	35°30'17"N	121°10'47"W	Mud, sand and boulders
4	Jan. 28, '78	107-218	35°40'15"N	121°20'30"W	Mud, sand and boulders
5	Jan. 29, '78	277-332	35°30'25"N	121°10'57"W	Mud, compacted mud boulders

Table 2

Species Composition of Trawls

Species	Trawl Number		
	2	4	5
Cephalaspidea			
Scaphandridae			
1. <i>Acteocina intermedia</i> Willett, 1928			X
Aglajidae			
2. <i>Aglaja</i> sp. indet.	X		
	(from stomach of spec. 4)		
3. <i>Chelidonura inermis</i> (Cooper, 1863)			X
Notoaspidae			
Pleurobranchidae			
4. <i>Pleurobranchaea californica</i> MacFarland, 1966	X	X	
Nudibranchia			
Doridacea			
Cadlinidae			
5. <i>Cadlina</i> sp.			X
Dendronotidae			
6. <i>Dendronotus frondosus</i> (Ascanius, 1774)	X		
	(from stomach of spec. 4)		

color and the foot was white.

An intact radula of *Dendronotus frondosus* (Ascanius, 1774) was also found in the stomach of this *Pleurobranchaea*. The radula agreed in every respect with that described in McDONALD (1977). This finding should establish the occurrence of *D. frondosus* at this depth in California waters. Its deepest occurrence in California is reported to be 19 m (SPHON & LANCE, 1968) and 40 m at Friday Harbor, Washington (ROBILLIARD, 1970). In the Atlantic, this cosmopolitan species is reported to 400 m (SWENNEN, 1961).

Also found in this stomach were 2 isopods, possibly juveniles of the suborder Flabellifera, copepod exuvia, many minute fish scales and sand and silt particles. The presence of fish scales would be expected from an animal which feeds by sucking its invertebrate prey off the mud surface.

The stomach of the *Pleurobranchaea* from trawl 4 contained several transparent "tunicate-like" organisms. They were too digested to allow for a more precise identification. The only other reports of food preferences of this species are COAN (1964) and CHIVERS (1966). However, these were laboratory observations and did not include prey species which would be available to *Pleurobranchaea* in nature.

The second collection, trawl 5 (Table 1), taken January 27, 1978 was in a depth of 277 - 332 m. Bottom substrate materials were mud and compacted mud boulders. Three opisthobranch species were collected in the trawl (Table 2). All 3 represent substantial depth extensions.

One specimen of *Acteocina intermedia* Willett, 1928, was collected in this trawl and later identified by Mr. Don Cadien, Marine Biological Consultants, Costa Mesa, California. The shell dimensions were 8 by 2 mm, length and breadth, respectively. SMITH & GORDON (1948) report *A. culcitella intermedia* to be common on sand bottoms, 18 - 55 m deep in Monterey Bay, California. WILLET (1928) reports this species in 55 m at Catalina Island, California. CARLISLE (1969) reports *A. intermedia* to be frequent in Santa Monica Bay, California, at depths from 37 - 184 m.

A single specimen of *Chelidonura inermis* (Cooper, 1863) was also collected in this trawl. The specimen measured 20 mm (preserved). Its colors were bright and typical. The specimen was in good condition, but its stomach was empty.

PAINE (1963) reported the greatest depth for this species to be approximately 100 feet [30 m]. Described by him as abundant in bays and sloughs, our collection indicates that this species occurs offshore in the deep benthos as well.

The presence of available food for this highly voracious predator is confirmed by the occurrence, in the same trawl, of 2 other opisthobranch species on which it is known to prey: *Acteocina intermedia* (previously discussed) and *Cadlina* sp. (Table 2).

The one specimen of *Cadlina* found in trawl 5 measured about 30 mm long and 15 mm wide (preserved). This species remains unidentified. We offer the following detail for future authors to use for the purpose of synonymy.

The dorsum was nearly smooth, bearing very low tubercles. The foot was long and linear and the labial tentacles were short and auriculate. The perfoliate rhinophores bore 14 lamellae. The entire body color (preserved) was cream, with no distinguishable markings common to *Cadlina*, such as dark rhinophores or dorsal spotting. The radular formula was $86 \times (34 - 36 \cdot 1 \cdot 34 - 36)$. The rachidian teeth bore 5 - 6 blunt denticles (Figure 2a). The innermost lateral teeth bore 1 - 2 denticles on the inner margin (Figure 2b). The 15th lateral tooth was hook-shaped with 11 - 14 denticles below a long cusp (Figure 2c). The outermost lateral tooth was without a cusp and bore 5 - 7 denticles beginning at its tip (Figure 2d).

While this description does not agree with any known California species of *Cadlina* (McDONALD, 1977), we

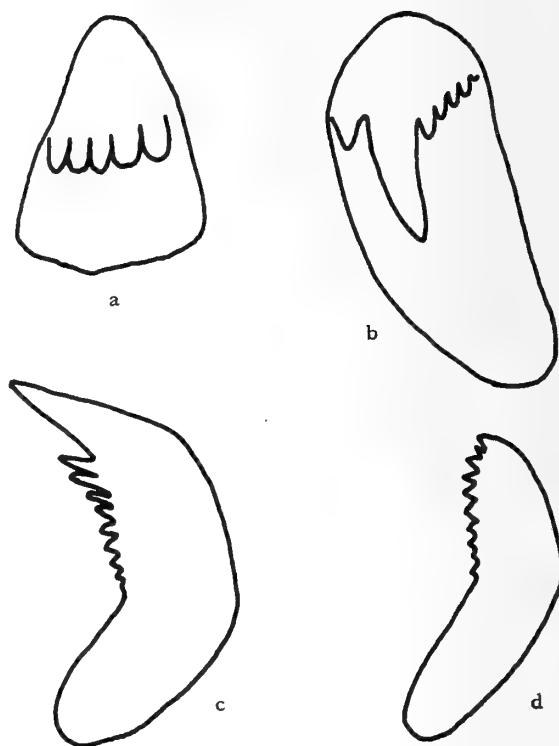


Figure 2

Radula of *Cadlina* sp. (from 40th row)

a - rachidian; b - 1st lateral tooth; c - 15th lateral tooth
d - 33rd lateral tooth

believe it most nearly agrees with *C. flavomaculata* MacFarland, 1905. The exceptions are the absence of dark rhinophores, and a slight deviation in radular morphology and a number of radular teeth. *Cadlina flavomaculata* is reported to a depth of 220 m (LEE & BROPHY, 1969). Their specimen, which was trawled off Port Hueneme, Ventura County, California, is no longer available for examination and there are no field notes to assist in confirming that identification and its possible alliance with our specimen. Prior to LEE & BROPHY (*op. cit.*) *C. flavomaculata* was known as an inshore species found only to 19 m (SPHON & LANCE, 1968). Due to the apparent difference in morphology, this specimen might well belong to an undescribed species. We are hesitant to formally describe this species without additional material.

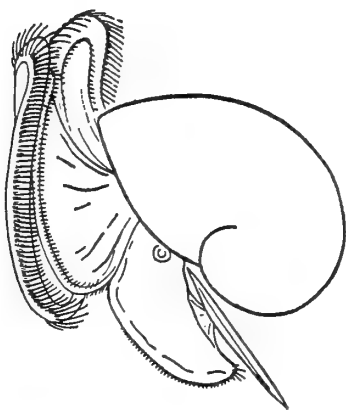
Stomach analysis found the gut empty.

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We would like to express our thanks to Mr. Gary Hopkins, skipper of the *Silver Queen*, for allowing the senior author to accompany him on this trip. Special thanks to Pacific Gas and Electric Company for the use of its Diablo Canyon Biological Research Laboratory and facilities for examining the trawl samples, and to Messrs. Bud Laurent and John Warrick for reviewing the manuscript. Thanks also to Mr. Don Cadien for his identification of *Acteocina intermedia* and to Messrs. Bob Henderson and Pat Brophy for their examination of the *Aglaja* specimen.

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Some Aspects of Food Intake in *Octopus joubini* Robson

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(3 Text figures)

INTRODUCTION

ENVIRONMENTAL FACTORS may affect an animal's food intake in a variety of ways, some of which may be affected by phylogenetic background or mode of life, some of which may be general. For instance, all animals should regulate the amount of food intake at one time by feedback signals, as DETHIER (1976) has shown for the fly. Yet predators have a set of demands which must affect their intake drastically – the necessity of searching for food, subduing and consuming it, and responding to temporary abundance. They may thus, for instance, have a very high "ceiling" for food intake and phylogenetic differences in their response to increasing density. HOLLING (1966) has postulated a general mode of predator intake dependent on density, and found intake of invertebrates could be described as a negatively accelerated curve rising to a plateau, and that of vertebrates as an S-shaped curve. He admits that these phylogenetic differences should arise because of the capability of vertebrates to learn, and that cephalopods could be similar to mammals. To look at this and other factors affecting food intake, octopuses are thus of interest and the small *Octopus joubini*, which can easily be kept in captivity, is an ideal species.

Information about food intake is available from experiments on rats (see HINDE, 1970), flies (DETHIER, 1976), and, in marine species, goldfish (ROZIN & MAYER, 1961) and three-spined stickleback. For octopuses, information on food intake comes from studies of several species in the genus *Octopus* and is fragmented and sometimes contradictory. Temperature affected food intake in *O. briareus*; with an increase of 10°C (20° to 30°), animals ate twice as much (BORER, 1971). Temperature influenced food intake of *O. vulgaris* as well, and again intake increased when temperature was higher (MANGOLD & VON BOLETZKY, 1973). Deprivation of food raised

intake in *O. maya* (WALKER, LONGO & BITTERMAN, 1970); intake after 2 days' deprivation was double that after one day's. However, deprivation only increased intake of *O. briareus* minimally (BORER, *op. cit.*). *Octopus briareus* was affected by prey density, however. BORER (*op. cit.*) recorded a linear increase in number of crabs eaten dependent on density, which does not fit HOLLING's (1966) model. However, she did not record weight of intake, which would be a clearer measure since octopuses do not always eat all of a killed prey. One factor, maturation of female octopuses to the egg laying and brooding stage, influenced animals of several species in the same manner. Female *O. cyanea* (VAN HEUKELEM, 1973), *O. maya* (WALKER *et al.*, 1970), *O. vulgaris* (MANGOLD & VON BOLETZKY, 1973) and *O. joubini* (OPRESKO & THOMAS, 1975) all nearly ceased food intake during brooding.

As might be expected of predatory animals, octopuses appear to be tolerant of long periods of food deprivation. Rats lost a larger percentage of body weight each day during deprivation (CAMPBELL, TEIGHTSOONIAN & WILLIAMS, 1961) than did octopuses. Furthermore, octopuses lost less weight per day over successive days of deprivation (NIXON, 1966; MANGOLD & VON BOLETZKY, 1973), whereas rats lost weight steadily. After deprivation and weight loss, *Octopus maya* were capable of a much increased intake of food (WALKER *et al.*, 1970), which would compensate for the period of deprivation.

The present study concerns factors affecting feeding and food deprivation in *Octopus joubini* Robson, 1929. These very small animals are ideal for laboratory investigation because they can be kept in small, closed salt water systems and have a short life span (THOMAS & OPRESKO, 1973). They can also be raised from eggs, as the relatively large young are benthic (VON BOLETZKY & VON BOLETZKY, 1969; MATHER, 1972; OPRESKO & THOMAS, 1975). Moreover, since most octopuses have

the same benthic predatory mode of life, parallels may be drawn between *O. joubini* and other octopod species. In this study, intake was studied when food was provided *ad libitum* and under varied conditions of deprivation and prey density, during females' egg production and brooding.

PROCEDURE

(a) **Maintenance:** Octopuses were collected from St. Joseph Bay, Florida (they were picked off the sandy bottom in their shell "homes") and flown, still in the shells, to Boston. In the laboratory they were isolated in 18 L or 36 L capacity aquaria with separate closed sea water systems. Each animal was given a 2.5 cm cube plexiglass "home" (4 sides dark, one end clear and one end open). Temperature was controlled separately in each tank and maintained at 23°C ($\pm 1^\circ$). Once each week, salinity was measured and corrected by addition of distilled water and $\frac{1}{3}$ of the water was changed to prevent the accumulation of nitrates. A bright white light provided illumination during the day and a dim red one at night. The changeover was timed to sunrise and sunset in Boston (in order to produce a daylength variation which might have been important for maturation), and corrected weekly.

(b) **Intake Estimation:** *Uca* fiddler crabs and *Nassarius* mud snails were used as prey. The number of prey provided was always in excess of expected intake estimated from previous findings. To ensure an accurate measure of intake, live crabs were first immersed in water, then dried on blotting paper for 10 seconds before being weighed (this procedure was carried out before they were offered as prey and again if they survived, after the octopuses' feeding period). Live and dead prey were removed after approximately 24 hours (*Octopus joubini* feeds almost exclusively at night, so small differences in amount of day time affected intake little). Bodies of crabs that had been partly eaten (or carapaces and arm bases if the crab had been disjointed) were allowed to drain on blotting paper 10 seconds before being weighed. Live snails were weighed the same way as live crabs, but the empty shells were held for 10 seconds with the siphon notch on blotting paper to ensure adequate drainage. Intake was measured by subtracting weight of prey (and shells) removed from weight of prey offered.

(c) Experimental Conditions:

(1) **Baseline** – Four octopuses were offered crabs provided *ad libitum* for 40 days. Their baseline intake and daily variations were recorded.

(2) **Deprivation** – A group of 4 octopuses was fed crabs after varied periods of deprivation. For 2 replications they were deprived 1, 2 and 4 days in a Latin Square arrangement (data for zero days' deprivation were collected from the *ad libitum* feeding of the day before and day after trials). As the major intake difference was between zero and one day's deprivation, the third and fourth replications used deprivation times zero, one, and four days in a Latin Square arrangement. During the third and fourth sequence, weight changes were monitored during the 4-day deprivation period. Each octopus' plexiglass "home" had been weighed damp before he used it. During each day of deprivation and after the octopuses were fed, each was weighed in his home. This procedure included a presumably constant error due to the weight of the water contained in the octopuses' mantle cavities, but minimized disturbance and produced stable results. The weight of each home was subtracted from the weight of octopus and home to calculate the weight of each octopus.

(3) **Density** – Density of prey species is one way of varying absolute quantity – it can also be varied by varying prey size. Three experimental manipulations were used to separate relative influences of the factors – varying prey size (numbers constant), varying prey number (size constant) and covarying prey size and number so that total prey weight was constant. All 3 tests were carried out using crabs as prey. The last mentioned manipulation was done first, and the design corresponds to BORER's (1971) design of alternating low density (4 crabs) with 4 higher densities (8, 10, 12, 16 crabs). Because this design, while a faithful copy of her experimental situation, is impractical for statistical analysis, the other tests were arranged differently. For weight variation ($n=16$) 3 levels (weight doubled and redoubled) were used, arranged in a Latin Square arrangement. For numbers variation ($n=11$) there were also 3 levels (number doubled and redoubled) in the same arrangement. Using snails as prey, only tests of size variation ($n=10$) and number variation ($n=13$) were carried out. Numbers were given at the same 3 levels, but size could only be doubled and was thus at 2 levels, because the size variation of the snails is less than that of the crabs.

(4) **Intake of Females during Egg Production and Brooding** – Four females who neared egg laying were provided food *ad libitum* throughout brooding and until death (#24 was in one 2-week density study prior to egg laying). Six males were also provided food *ad libitum* as a control. Females' food intake was charted according to time preceding or following egg laying (they did not all lay eggs at the same time), males' by the calendar.

RESULTS

(a) **Baseline:** Four juvenile octopuses were given excess crab prey and still showed a marked variation in daily intake with no consistent pattern across individuals which would suggest environmental influences such as water quality. As Figure 1 shows, intake could be relatively constant or cyclic, and could drop to zero for up to 3 days. There was no consistent pattern of intake from day to day but the mean intake of each animal was similar when averaged over a 10-day period, and the mean for all animals rose slowly from 0.9g/day in the first 10-day period to 1.2g/day in the 4th 10-day period, as the animals grew.

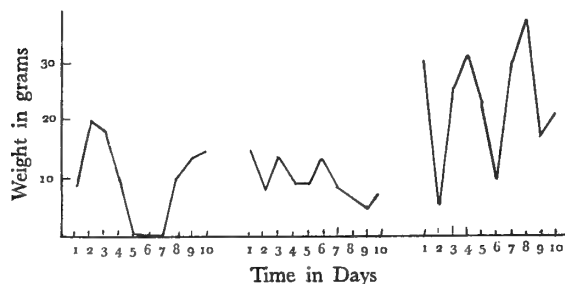


Figure 1

Some examples of patterns of daily food intake in grams for *Octopus joubini* provided crab prey *ad libitum* ($n=4$)

(b) **Deprivation:** Lack of food for even one day markedly influenced intake. Mean food intake of 4 octopuses after zero days' deprivation was 0.212g, after 1 day's deprivation 0.396g; this difference was significant at the $p < 0.01$ level in a t-test of difference between paired observations. Mean intake after 4 days' deprivation was 0.494g, which was not significantly different from intake after one day's deprivation.

Weight Loss During Deprivation: Juvenile octopuses lost weight slowly during food deprivation. After 4 days, weight loss averaged 10% of body weight, but daily loss declined from 5% the first day to 1% the last (Figure 2). After 4 days' deprivation, the octopuses ate to excess and body weight rose to 105% of that before deprivation.

(c) **Density:** Influence of prey density on food intake depended on prey species (Table 1). With crab prey and variation of prey size (prey number = 12), intake varied from 0.45g with 3g of prey, to 0.68g with 6g of prey and 1.35g with 12g of prey ($n = 16$). These values are significantly different at the $p < 0.01$ level in an analysis of variance.

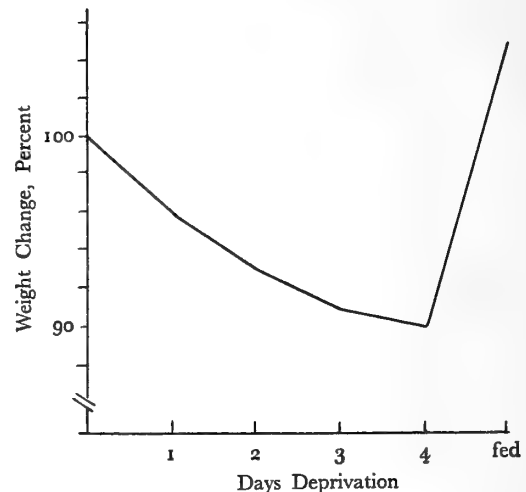


Figure 2

Percentage change in body weight of *Octopus joubini* over 4 days of food deprivation and after 1 subsequent day with excess crab prey ($n=4$)

ysis of variance. With crab prey and variation in number (size constant), octopuses offered 6 ate an average of 0.51g, when offered 12 ate 0.81g and when offered 24 ate 1.07g ($n = 11$). These differences are significant at the $p < 0.05$ level in an analysis of variance. With crab prey, and number and weight covarying so that total weight was constant (2.25g), the octopuses ate 0.22g with 4 crabs, 0.23g with 8, and 0.18g with 10, 0.17g with 12, and 0.26g with 16 crabs ($n = 4 \times 2$ replications). These differences are not significant in an analysis of variance (overall intake values are smaller in this test because the octopuses were younger).

With snail prey, the results were different. When prey number was constant ($n = 10$) but prey size varied, octopuses ate 0.40g of 0.7g snails and 0.56g of 1.4g snails ($n = 11$). This difference is not significant by a t-test of differences between paired observations. When prey size was constant (1.1g) but prey number varied, the octopuses ate 0.68g of 10 snails, 0.70g of 20 snails and 0.96g of 40 snails ($n = 13$). These differences are not significant in an analysis of variance.

(d) **Intake of Females during Egg Production and Brooding:** Because the 4 females that laid eggs did so at different times, their intake was averaged over week periods before and after egg laying (e. g., week before, 2

Table 1

Effect of Prey Density of Crab and Snail Prey
on Weight of Food Intake of *Octopus joubini*

Prey Type	Prey Number	Prey Unit Weight (gm)	Prey Total Weight (gm)	Mean Intake Weight (gm)
Crab	4	0.56	2.25	0.22
	8	0.28	2.25	0.23
	10	0.22	2.25	0.18
	12	0.19	2.25	0.17
	16	0.14	2.25	0.26
Crab	6	0.58	3.50	0.51*
	12	0.58	7.00	0.81
	24	0.58	14.00	1.07
Crab	12	0.25	3.00	0.45**
	12	0.50	6.00	0.68
	12	1.00	12.00	1.35
Snail	10	0.70	7.00	0.41
	10	1.40	14.00	0.56
Snail	10	1.10	11.00	0.68
	20	1.10	22.00	0.70
	40	1.10	44.00	0.96

*ANOVA $p < 0.05$

**ANOVA $p < 0.01$

weeks after). Average intake of females rose 3 weeks before egg laying to nearly 1.0g/day, fell the week before to 0.57g/day (this is within the range of male food intake at this time), and then fell to under 0.20g for most of the 6-week brooding period (Figure 3). Average food intake by 6 males during this period ranged from 0.29g/day to 0.47g/day.

DISCUSSION

Several aspects of the food intake of *Octopus joubini* are typical of predatory animals. The wide variability in daily intake despite a constant food supply is also characteristic of predatory goldfish (ROZIN & MAYER, 1961), stickleback (TUGENDHAT, 1960), and blowflies (DETHIER, 1976: 283), but unlike constant intake of omnivorous rats (CORBIT & STELLAR, 1961). *Octopus vulgaris* also varies its intake, from low to high on alternate days (Wodinsky, personal communication). The ability to tolerate and

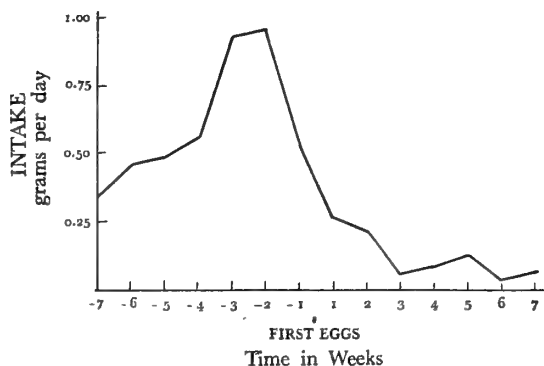


Figure 3

Weight of food intake in grams of female *Octopus joubini* eating crab prey, averaged over week-long periods measured before and after egg laying ($n=4$)

compensate for deprivation shown by *O. joubini* is also an advantage for a predator. These octopuses tolerated 4 days' deprivation with a weight loss of only 10%, and the loss per day declined with increasing deprivation. This loss was larger than that of *O. briareus* for the same deprivation time (6%) (BORER, 1970) and than that of *O. vulgaris* (4%) for 6 days (MANGOLD & VON BOLETZKY, 1973), perhaps because the smaller *O. joubini* is metabolically more active. Both *O. joubini* and *O. vulgaris* (MANGOLD & VON BOLETZKY, *op. cit.*) compensated for long periods of deprivation by eating so much (up to 20% of body weight for *O. joubini*) that weight loss was quickly recovered.

Food deprivation for even 1 day affects *Octopus joubini*'s food intake. This agrees with TUGENDHAT's (1960) observations for stickleback and WALKER, LONGO & BITTERMAN's (1970) observations for *O. maya*, though intake increased for all 3 species after 1 or 2 days' deprivation. BORER (1970) found only a minimal effect of deprivation on food intake for *O. briareus*.

The data on food intake show two results. First, *Octopus joubini* are consistent in their intake response to absolute quantity of crab prey. When crab prey size and weight were co-varied so weight was always 2.25g, intake did not vary significantly. Second, *O. joubini* were affected by both increased crab size and by increased crab weight. As for *O. cyanea* (BOUCHER-RODONI, 1973) and for rats (BALAGURA & HARRELL, 1974), *O. joubini*

increased food intake when the weight of units offered was greater. The rise in weight of food intake with increased crab prey density for *O. joubini* was not linear, as BORER (1971) found for number of crabs eaten with *O. briareus*. Instead, it apparently begins to negatively accelerate, as suggested by HOLLING (1966) for intake of predators with increased prey density.

The response to snail prey is less easy to interpret, since snails are less preferred prey for *Octopus joubini* (MATHER, 1972) and also time-in-contact (see HOLLING, 1966) will be less for them than for crabs. This is true because crabs are more active than snails. Wodinsky (personal communication) was able to remove the "density effect" on *O. vulgaris* by confining crab prey. It is also true because *O. joubini* spent a long period pulling snails out of their shells before consuming them, but could kill and begin to eat a crab in one minute. Perhaps time-in-contact with snails is small enough that *O. joubini*'s intake was at the base of the S-shape curve suggested by HOLLING (1966). Perhaps, as in BEUKEMA (1968), the density effect is complicated by prey preference.

The reproductive state of females also affected their food intake. An intake decline before and during brooding is common among octopods, mentioned for *Octopus joubini* by OPRESKO & THOMAS (1975), for *O. vulgaris* by NIXON (1966), for *O. cyanea* by VAN HEUKELEM (1973) and for *Haplochalaena maculosa* by TRANTER & AUGUSTINE (1973). It is interesting that the decline in food intake began before egg laying – one week before for *O. joubini*, 2 to 8 weeks before for *O. vulgaris* (MANGOLD & VON BOLETZKY, 1973) and several weeks before for *O. cyanea* (VAN HEUKELEM, 1973). But no octopod yet studied other than *O. joubini* has shown increased intake and a growth spurt before egg laying. This pattern may be related to *O. joubini*'s short life span or to its very small size (the weight of eggs becomes a large proportion of body weight); it parallels the growth spurt of juvenile female *O. vulgaris* when control over their optic glands was removed and they matured early (WELLS & WELLS, 1959). The effect may be a hormonal one, high intake being induced by optic gland hormones.

Octopus joubini's food intake and feeding appear fairly typical of octopods. Deprivation of food caused elevated intake and weight loss which declined with time, as for other octopods. Density increase and weight increase caused increased intake, a result similar to, but not the same as, that in other *Octopus* species. Changes in female reproductive state cause first an increase and then a decrease in food intake. Only the latter effect has been previously noted in octopuses, perhaps because *O. joubini*'s short life span compresses and clarifies long-term effects. For this reason, and because these small animals are easy to maintain in the laboratory, *O. joubini* offers

an excellent opportunity for future research on feeding and food intake.

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Predation by a Rockfish, *Sebastes chrysomelas*, on *Lamellaria diegoensis* Dall, 1885

BY

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THE LAMELLARIDAE REPRESENT a family of marine mesogastropods that apparently rely upon cryptic adaptations (GHISELIN, 1964; THOMPSON, 1973) and defensive acid secretions (THOMPSON, 1960; 1969) to avoid detection and falling prey to a variety of predatory fish and invertebrates. These gastropods can mimic their own prey organism, compound ascidians, as well as other invertebrates not commonly taken by predators, *e. g.*, barnacles (GHISELIN, *op. cit.*; THOMPSON, 1973). These adaptations, as well as the production of strong defensive acidic fluids (approximate pH = 1) have been thought to preclude predation of these gastropods by fishes, which THOMPSON (*op. cit.*) states "... are known to detest food which tastes acidic ..."

On August 15, 1977 a female specimen of *Sebastes chrysomelas* (Jordan & Gilbert), measuring 245 mm, was collected during a food habits study in the vicinity of Diablo Canyon, San Luis Obispo County, California (120°51'23"W; 35°12'44"N). In the stomach contents of this individual was a single specimen of *Lamellaria diegoensis* Dall, 1885, the only prey item present. Past experience with 80 specimens of *S. chrysomelas* collected during the present study, as well as observations by LARSON (1972), had shown an apparent preference by this rockfish for *Octopus* spp. and small decapod crustaceans.

The occurrence of *Lamellaria diegoensis* thus represents a unique food item never before documented. This raises several questions as to the location of the lamellarid when it was taken, and the feeding behavior of the fish:

1. Was the lamellarid residing on a tunicate when attacked by the fish?
2. If the lamellarid was mimicking an ascidian, how was it detected by the fish?
3. Why would the fish feed on a prey so foreign to its usual diet, especially one that is capable of secreting strongly acidic fluids?

Field observations indicate that *Lamellaria diegoensis* was observed most commonly on substrates other than compound ascidians (David Behrens, Diablo Canyon Research Laboratory, personal communication). In these instances the lamellarid failed to mimic the substrate and was clearly visible. These observations could explain how the lamellarid was observed by the fish; however, the question of why the fish fed on the lamellarid, which can secrete strong acidic fluids, still remains. Continuing laboratory and field observations may provide the answer.

ACKNOWLEDGMENTS

I would like to thank Pacific Gas and Electric Company for permission to release this information. This study was funded through a contract with Lockheed Center for Marine Research.

I am also grateful for the critical review of this manuscript by David Behrens and his positive identification of the specimen.

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Observations on Spawning in *Calliostoma ligatum* (Gould, 1849)

BY

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ALTHOUGH THE GENUS *Calliostoma* occurs commonly along the Pacific Coast of North America, the life histories of these trochids remain virtually unknown. Recently, several authors have contributed to the natural history of these snails: KEEN (1975) provided observation on morphology and habits of several *Calliostoma* from California; PERRON (1975) reported on the feeding behavior of 3 Oregon species of *Calliostoma*; LOWRY, McELROY & PEARSE (1974) discussed distribution and habitat preference in a shallow subtidal environment at Monterey, California; SELLERS (1977) and HUNT (1977) discussed behavior and distribution of *Calliostoma* inhabiting kelp beds in central California. Spawning behavior of the California species has not been previously documented.

On July 18, 1977, a single specimen of *Calliostoma ligatum* (Gould, 1849) was collected during a shallow water (3.6m) settling plate study at Diablo Canyon in San Luis Obispo County, California (120°51'23"W; 35°12'44"N). The animal was maintained in a container of seawater. The snail immediately moved to the water-air interface and remained stationary for 20 minutes, after which time green eggs were extruded from the right side of the mantle cavity. The eggs were liberated in a mucus sheath in groups of 10 to 12. Within 25 minutes the bottom of the aquarium contained large masses of green eggs. The spawning lasted for 2 hours and 3 minutes, at which time the total number of eggs spawned was estimated at approximately 3 000. Each egg was spherical, 29 - 30 μ m in diameter. The granular green eggs had a single central yolk sac.

Similar spawning behavior has been observed for another trochid, *Tegula brunnea* (Philippi, 1848), collected in Oregon during August (BELCHIK, 1965). Spawning occurred approximately 12 hours after collection in both

male and female specimens of *T. brunnea*. The males were observed to "... discharge puffs of white sperm," followed by spawning of moss-green eggs by the females. No male *Calliostoma ligatum* occurred on the settling plate on which the female specimen was found; however, these snails are common in the area and the possibility of spawning induced by a nearby male does exist. Spawning may also have been induced by the stress of being transferred from the field to the laboratory, or by some other, unknown factor.

ACKNOWLEDGMENTS

I would like to thank Pacific Gas and Electric Company for permission to release this information. This study was funded through a contract with Lockheed Center for Marine Research.

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NOTES & NEWS

Trematodes in Chilean Fissurellid Molluscs

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MOLLUSCS ARE CLASSICALLY described as intermediate hosts for trematodes. Larval trematodes have been found in a number of gastropod species. In spite of this general statement, one of the authors found adult trematodes in the gonads of *Fissurella crassa* Lamarck, 1822 in January 1976. After this discovery, we investigated the other large-sized *Fissurella* species living on northern Chilean coasts and we found these trematodes in the gonads of all of them.

We have collected specimens of 8 species of *Fissurella* from several localities in northern Chile, situated between 20°16'S, 70°09'W and 20°41'S, 70°11'W, from January 1976 until September 1979. The animals examined varied in shell length from 25.3 mm to 111.2 mm. The results of this study are summarized in Table 1. Samples of trema-

Table 1

Number of analyzed animals of each species
of *Fissurella* and percentage of infected specimens.

Species	N	% infected animals
<i>Fissurella</i>		
<i>bridgesii</i> Reeve, 1849	35	71.43
<i>costata</i> Lesson, 1830	29	27.58
<i>crassa</i> Lamarck, 1822	136	13.97
<i>cumingi</i> Reeve, 1849	353	64.87
<i>latimarginata</i> Sowerby, 1835	46	54.34
<i>limbata</i> Sowerby, 1835	36	47.22
<i>maxima</i> Sowerby, 1835	231	96.97
<i>pulchra</i> Sowerby, 1835	138	77.53
TOTAL	1004	

todes from each species of *Fissurella* were examined. With the kind assistance of Dr. J. B. Jones of the Ministry of Agriculture and Fisheries, New Zealand, they were identified as digenetic trematodes belonging to the family Fellodistomidae and to the genus *Proctoeces* Odhner, 1911.

The effect of parasitization on the reproduction of the hosts is now being studied in our laboratories.

The importance of the present report is to make known the fact that gastropod molluscs can be hosts to adult digenetic trematodes. It is, thus, evident, that not only trematode larvae may be present in molluscs.

Fissurella species are economically important in Chile because they are eaten by people. As far as we know, the trematodes mentioned above do not affect man; thus, their presence is not dangerous for man. Nevertheless, it should be noted that only the foot of the fissurellids is eaten; the viscera are always discarded.

ERRATA

Dr. Howard M. Feder has requested that we call the attention of our readers to the following errors which escaped the proof readers:

page 182, in the first paragraph of "Materials & Methods" change January 1 to January 20; May 7 to May 18 (both 1973); and January 20, 1974 to January 26.

In Figures 3 and 4 on pp. 185 and 186, respectively, the numbers in parentheses below months refer to dates; numbers in parentheses below boxes represent numbers of clams.

New Rate Schedules

At its regular meeting on October 17, 1979, the Executive Board of the Society, after a careful evaluation of the financial situation, came to the conclusion that an adjustment in the subscription and dues schedules could no longer be avoided. This necessity was underscored by the fact that the volume-year 1978/1979, in spite of several generous donations received and stringent economizing, brought in effect a deficit of over \$9000.00. Consequently, it was decided to increase the membership dues for members residing in the U.S.A. to \$18.50; subscription rates for addresses in the U.S.A. are increased to \$37.50; in both cases a charge of \$1.50 for postage must be added.

On the other hand, the rates for members and subscribers in all foreign countries can be kept the same as that charged for volume 22, *i. e.*, Swiss Francs 30.00 for dues, Swiss Francs 60.00 for subscriptions, plus, in all cases, Swiss Francs 7.00 for postage. We have learned that it is impossible in some countries to obtain checks in Swiss Francs; in such cases, the equivalent amount at the exchange rate, effective when the remittance is being made, in U. S. \$ will be acceptable. However, we must insist that all remittances be made in a form that will not cause any expense to the Society as banks may charge as much as \$5.00 for "collecting". It should be obvious that we are absolutely unable to absorb such fees.

We deeply regret the necessity of increasing the dues and subscription rates; our optimism that inflation would be curbed has proven unjustified. We can not fight this trend alone.

We must emphasize that under no condition can we accept subscription orders or membership applications for calendar year periods. If "split volumes" are required, we must charge the individual number costs. Individual issues sell at prices ranging from US\$12.00 to US\$30.00, depending on the cost to us.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.-face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US\$18.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims for missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues.

This refusal is necessary as we have received an increasing number of "claims" as much as 6 months before the claimed issue was to be published. We wish to conserve our energy and the cost of postage and stationery for more productive purposes.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

REGARDING POSTAL SERVICE

We are much disturbed by the steadily increasing number of premature claims for supposedly "missing" issues of our journal. Since we have announced on numerous occasions that our journal is mailed on the dates printed in the issues, *i. e.*, number 1 on July 1, number 2 on October 1, number 3 on January 1 and number 4 on April 1 of each volume year, it is unreasonable to expect delivery of the issues earlier than at least one week after these dates; however, a much longer time must be allowed for delivery to addresses at various distances from Berkeley. Thus, for example, a two weeks lapse is not unusual for as short distances as 500 km; and up to 3 and 4 months must be counted on for addresses in the Far East and in Africa. We are faced with the alternative of not replying to what we must consider premature claims or, if the trend continues, we must increase our subscription rates to cover these additional expenses. Our past efforts at keeping the subscription rate as low as possible are, we believe, sufficient evidence that we simply cannot afford any other course of action. The postal service causes us enough

financial losses. Therefore we urgently request that before a claim is made, the time schedule be carefully checked. We are grateful for the understanding of this difficult situation shown by many librarians and will be grateful to those who, heretofore being perhaps eager to make sure that the library receives what is coming to it, will exercise a little patience.

Your harassed Editor.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper covered and cloth bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA (lifornia) 93644, at the prices indicated in our Notes and News section, plus postage and, where applicable, California State Sales Tax. The same will apply to the Supplements that are still in print, except for supplements to vol. 7 (Glossary) and 15 (Ovulidae), which are sold by The Shell Cabinet, P. O. Box 29, Falls Church, VI (rginia) 22046; and supplement to volume 18 (Chitons) which is available from Hopkins Marine Station, Pacific Grove, CA (lifornia) 93950.

Volumes 1 through 8 and 10 through 12 are out of print.

Volume 9: \$22.- - Volume 13: \$24.- - Volume 14: \$28.-
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Volumes 17 to 20: \$34.- each; Vol. 21: \$40.-. Postage and handling extra.

There is a limited number of volumes 9, 11, 13, 14 to 20 available bound in full library buckram, black with gold title. These volumes sell as follows: 9 - \$27.-; 11 and 13 - \$29.- each; 14 and 15 - \$33.- each; 16 - \$38.-; 17, 18 and 19 - \$41.75 each; 20 - \$42.25; 21 - 48.75.

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Supplement to Volume 3: \$6.-

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspidæa of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

[The two parts are available separately at \$3.- each]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announcement elsewhere in this issue.

Supplement to Volume 11: \$6.-.

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14: \$6.-.

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16: \$8.-.

[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

Orders for any of the publications listed above should be sent directly to Mr. Art West. If orders are sent to us, we will forward them. This will necessarily result in delays.

Other supplements:

A Glossary of A Thousand-and-One Terms Used in Conchology

by WINIFRED H. ARNOLD

originally published as a supplement to volume 7 of the Veliger has been reprinted and is now available from The Shell Cabinet, Post Office Box 29, Falls Church, Virginia 22046, U. S. A. The cost is US\$ 3.50 postpaid if remittance is sent with the order.

[A systematic Revision of the Recent Cypræid Family
Ovulidae by CRAWFORD NEILL CATE]

Supplement to Volume 15: Our stock is exhausted, but copies are still available from The Shell Cabinet, P. O. Box 29, Falls Church, Virginia 22046.

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA (lifornia) 93940.

Supplement to volume 18: \$10.50 postage paid.

[The Biology of Chitons by Robin Burnett *et al.*].

(Our supply of this supplement is exhausted; however, copies may be available by making application to the Secretary, Hopkins Marine Station, Pacific Grove, California 93950.)

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

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Supplement to Volume 6: \$1.50; to Volume 18: \$3.00

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Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, 792 Laurie Avenue, Santa Clara, CA 95050.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA (lifornia) 93644. Orders should be sent directly to Mr. West.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list will be presented in a forthcoming issue in the Notes and News section.

These individual issues will be available only directly from the Society. Details on how to order such copies will be given when the list is published.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

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accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

CALIFORNIA

MALACOOLOGICAL SOCIETY, Inc.

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BOOKS, PERIODICALS, PAMPHLETS

The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae

by GEORGE M. DAVIS. 120 pp.; 34 figs; 15 tables. Monograph no. 20, The Academy of Natural Sciences of Philadelphia, 19th and Parkway, Philadelphia, PA 19103. US\$12.00 1979

This monograph is a very good work on a very difficult subject. One can not imagine a more difficult gastropod group to deal with than snails which are all tiny, less than 5 mm long generally, with shells that show no easy identifying features. The anatomy of such small snails is just beyond the point of easy dissection with conventional tools and often necessitates serial sectioning. The author is also to be commended for his very modern, up-to-date treatment of this systematic group, taking into account multivariate analysis, plate tectonics, etc.

Basically, this work deals with the pomatiopsid subfamily Triculinae, in the southeast Asian river systems, whose members were previously assigned to that frequent dumping ground for unknown small prosobranchs, the

Hydrobiidae. In this pomatiopsid subfamily, the author finds that there are 11 genera and 92 species, making it possibly the largest contemporaneous endemic freshwater fauna of any known lake or river system. This group of organisms was previously considered of the Hydrobiidae and not of the Pomatiopsidae because of the convergence of such structures as the shell, radula, penis, and operculum! (In this list of convergent characters one can see the usual favorite morphological entities employed for most of the known taxonomic studies and assignments.) Davis found that the amount of convergence toward the Hydrobiidae had been greatly underestimated and is revealed in this group only by a study of the female reproductive system as a whole.

The origin of this fauna is now thought to have been Gondwanaland and that it was introduced into Asia by the collision of the Indian land mass with Asia. The subsequent Himalayan orogeny, resulting in streamcapturing to form the great river drainages of the southeastern part of Asia, probably caused the ancestral forms of the Triculinae to be introduced into the (apparently) virgin river systems. The net long term result was an apparently rapid and abundant burst of speciation, resulting in today's rich triculine fauna which went unrecognized as such until the present study.

There are a few errors - mostly minor - in this treatise. One type of error is exemplified by page 100, in the reference to Krull, 1935, where "An atomische" is used instead of the correct "Anatomische." In another case, in Appendix IV, the heading "Tribe Lacunopsini, Description of Taxa" is completely omitted, resulting in the inadvertent placement of "*Lacunopsis* Deshayes, 1876" within the tribe Triculini. On page 37, the states of Croatia, Slavonia, Dalmatia, Serbia and Bosnia are described as "districts of Yugoslavia and Hungary," where in actual fact none of these districts is located in Hungary; all are in Yugoslavia.

My major complaint is about what is perhaps the most important figure in the entire work, that of figure 3 on page 10. There is a number of cases where important structures are not labeled in figures C and E. Figure 3E is especially unclear in a number of respects. The relationship or connection between the bursa and the spermathecal duct (sd) is completely unclear since the duct which is labeled "sd" disappears under the oviduct and seminal receptacles. Is there a sperm duct in this figure? Also, there should have been presented here a renopericardial opening since it is essential to the discussion of sperm routes, but no such structure is drawn or indicated. The significance of two tiny, unlabeled protuberances arising from the pericardium is also lost on the reader.

With respect to figure 3E again, the author states on page 17 that the "major unifying character of the Triculinae is the spermathecal duct extending from the bursa copulatrix to the posterior end of the mantle cavity (Fig. 3C-E)." If one looks at figure 3E, this criterion is clearly not satisfied by the Lacunopsini. The entire figure 3 should have been drawn much larger and more accurately with respect to enabling one to trace the various ducts.

In another case, figure 18 on page 31 would have greatly benefitted by the inclusion of the bursa copulatrix in each figure. An extended legend which would explain the various drawings and their relationships, placed immediately next to the figure, would also have been most welcome.

There are some general points which the author could have cleared up for the reader. For example, where are the ova fertilized (if known)? On more general terms, a brief statement about the known or presumed functions of the various intricate parts of the female reproductive complex would have been of tremendous help for a general understanding of what is actually going on in these organisms. Moreover, the reader can not help but wonder what is the author's opinion about the significance of such large variety in the female anatomies of the Triculinae, especially in light of the fact that the author states that the male reproductive systems are so similar. If indeed the female genital systems are so varied and involved, is it really possible that the eggs of the various triculine species and genera are "so similar" that they can not be told apart at all (page 70)? One wonders how closely the eggs were examined, especially since there are no illustrations of them. (Even if the eggs are all covered by similar sized grains of sand, this does not preclude the possibility that the egg case shape or surface sculpture, etc., could be species specific.)

There are a few highly speculative or weakly argued statements. For example, on page 41, the author states that "Yet other complexities such as spiral-noded sculpture or reticulate sculpture might evolve for species recognition in sympatry . . ." Is there some factual basis for this kind of statement which could be cited or is it merely abstract or unfounded speculation, as it seems to be? An example of a weak argument occurs on page 44, where Davis first states the fact that "because of convergent evolution one cannot assume that if two fossil shells look alike they housed closely related animals," but then later in the same paragraph states that "if several species of an endemic fossil assemblage *appear to have survived* to the present in the same region, there is a good probability that there is a *phyletic connection* between the living taxa and the phenetically similar taxa" (italics by me, A. T.). Even in the context of the rest of

the page, this seems to be a circular argument or very close to one.

However, I do not mean to be overly critical. Despite my few criticisms, the author is to be congratulated for having done a very significant work on a broad basis. This publication will be of interest not only to the few specialists in this field, but should attract the attention of all malacologists generally interested in molluscan evolution because of its approach, style and contents.

I recommend this work highly in spite of its apparent high price (\$12.00) which it commands.

Alex S. Tompa
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University of Michigan
Ann Arbor, MI 48109

Bivalve mollusks of the western Beaufort Sea

by F. R. BERNARD. Contributions in Science, Natural History Museum of Los Angeles County, no. 313. 80 pp.; 112 figs. \$8.00, plus \$1.25 postage and handling. 31 July 1979.

The Beaufort Sea comprises Alaska's Arctic shore. This paper summarizes work by the Oregon State University School of Oceanography, mainly dredgings at depths of 20 to 2500 m on the continental slope of that area. It includes also some notice of along-shore collections made by others.

A total of 58 bivalve species are recognized, about half being of Pacific origin, half Atlantic. A key to the 22 families is given, as also keys to genera and subgenera within some families. All of the species are illustrated by half-tone photographs of good quality. Interiors of the right valves for the type species of each genus are shown in line drawings.

One new genus, *Boreacola*, is proposed, in Montacutidae. Its type species, *B. vadosa*, also is proposed as new. A second new species is *Axinulus careyi*, in Thyasiridae.

The list of publications in Literature Cited runs to nearly 12 pages – a good working bibliography on the Arctic Pleistocene and Recent molluscan fauna. An ingenious Appendix gives exact locations, by geographic coordinates and depth, and the repository and catalogue number for each specimen figured.

This is an admirably organized and compact report that gives the essential information on morphology and distribution for the taxa discussed.

A. Myra Keen

Our attention has been called to the fact that certain figures in the paper by Patrick M. Arnaud and Jean-Jacques van Mol in our July issue became, during the process of printing the entire issue, very blurred. As it is impossible for us to ascertain who received such defective pages, we include herewith replacement pages with our apologies and those of the printer.

Anatomy, Ecology and Distribution of the Volutidae and Volutomitridae of the Southern Indian Ocean

(Gastropoda: Prosobranchia)

BY

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AND

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(1 Plate; 10 Text figures)

THREE RECENT BENTHIC SURVEYS have been done with the M/S *Marion-Dufresne* in the subantarctic waters of the Indian Ocean. During cruise MD.03 (1974) several stations were made (including 50 macrobenthic samples) off Kerguelen, Heard and Crozet Islands between shallow water and 4200 m. Cruise MD.04 (1975) concentrated on the shelf around Kerguelen Islands, with 231 macrobenthic samples, and cruise MD.08 was mostly concerned with the Marion-Prince Edward shelf (49 macrobenthic samples) and the Crozet shelf (99 macrobenthic samples).

We collected 3 species of volutid and volutomitrid gastropods at 65 stations, in 73 samples, by trawls, dredges and grabs (Table 1): *Provocator pulcher* Watson, 1882; *Volutomitra curta* (Strebel, 1908) and *V. fragillima* Watson, 1882 (Figures 1 to 3). Study of the plentiful specimens provides the first thorough insight into these 2 allied neogastropod families in this area. Many faunistic and biogeographic data are recorded and the resulting distribution of the 3 species obtained is mapped (Figures 7, 8). Our anatomical studies, made with the help of D. van Weert, have led to discussion of several of their characteristics and assessment of their positions in the 2 families involved. The egg capsule of the volutid *Provocator pulcher* is also described and figured for the first time.

Family Volutidae

Provocator pulcher Watson, 1822

Provocator pulcher WATSON, 1882: 330, 331; 1886: 260, pl. 13, fig. 5; CARCELLES, 1947: 6; POWELL, 1960: 156; WEAVER & DUPONT, 1970: 123, fig. 53 F-G; CLOVER, 1975a: 10, 1 photo; 1975b: 1, 1 photo
Provocator provocator SOWERBY, 1887: 305, pl. 18, fig. 176; SMITH, 1942: 62, 63, pl. 13, fig. 95
Zidona (Provocator) pulchra. WENZ, 1943: 1350, fig. 3822

Specimens (empty shells recorded in parentheses):

- Kerguelen Islands

MD.03: 7-CP₄, 3; 11-CP₇, (2); 13-CP₉, 3; 17-CB₅, 12 (3); 21-CP₁₄, 5 (2); and 2 egg capsules (incl. 1 empty); 24-CB₆, 5 (1)

MD.04: 7-CP₁₃, 1 (2); 26-CP₆₁, 2; 34-DC₈₈, (1); 35-DC₈₉, 1; 38-CP₉₂, 1; 39-DC₉₃, (1); 45-DR₁₀₆, (2); 70-CP₁₆₉, 1 egg capsule; 95-DC₂₃₃, 1 egg capsule; 118-CP₂₈₄, 1 (1)

- Crozet Islands

MD.08: 42-CP₁₉₇, (1); 75-CP₃₀₃, (3); 78-CP₃₁₉, (2)

Distribution (Figures 7, 8):

The type locality is Kerguelen Islands, West Christmas Harbour, 48°43'S; 69°15'E, 105 fathoms [190 m], volcanic mud. Previously known only by empty shells (WATSON, 1882) and by shells from unknown stations off Kerguelen (CLOVER, 1975a, 1975b), the species is here re-

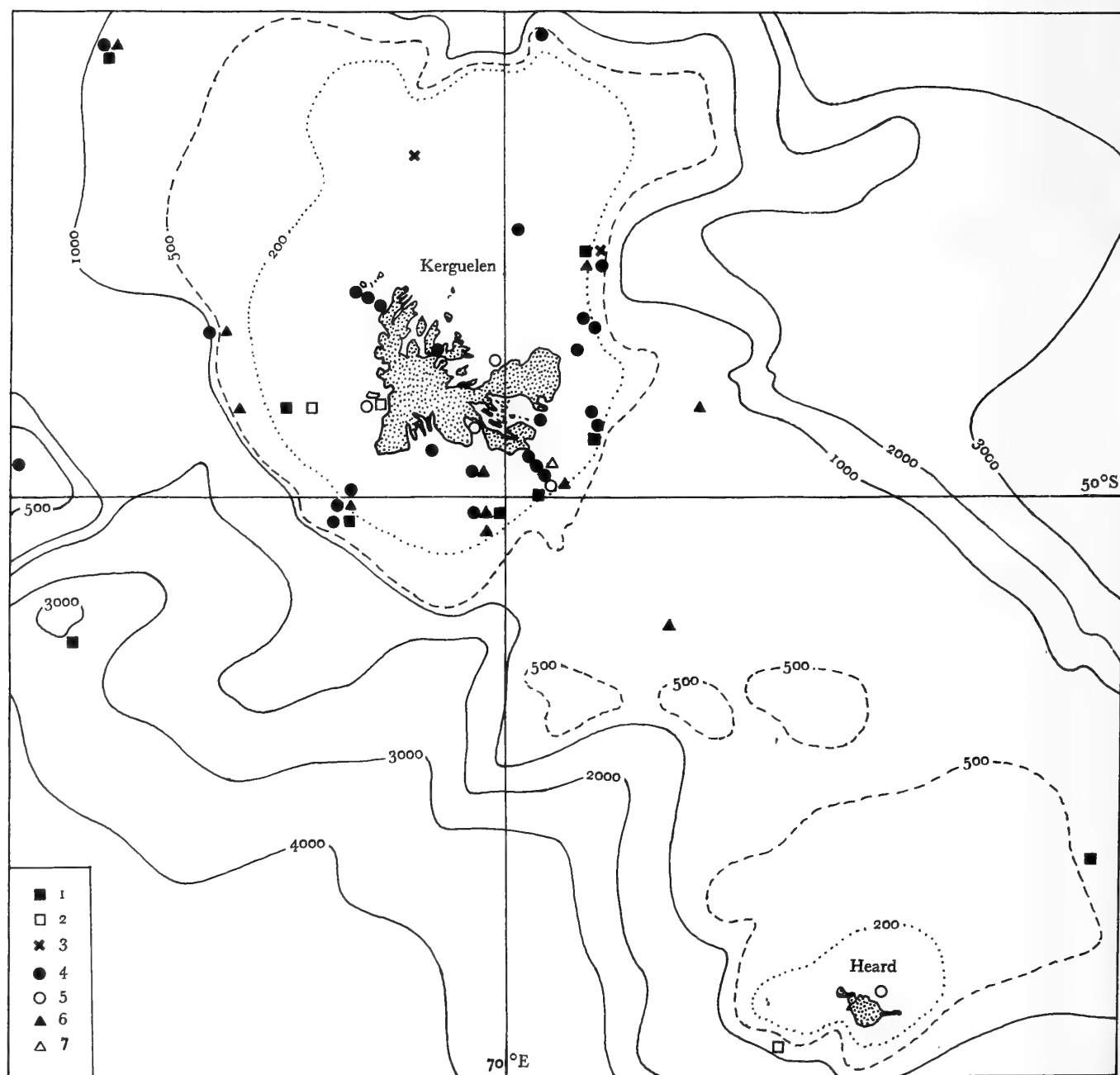


Figure 7

Present records of Volutidae and Volutomitridae off Kerguelen Islands and Heard Island: *Provocator pulcher* (1: living; 2: dead; 3: egg capsule), *Volutomitra fragillima* (4: living; 5: dead) and *Volutomitra curta* (6: living; 7: dead)

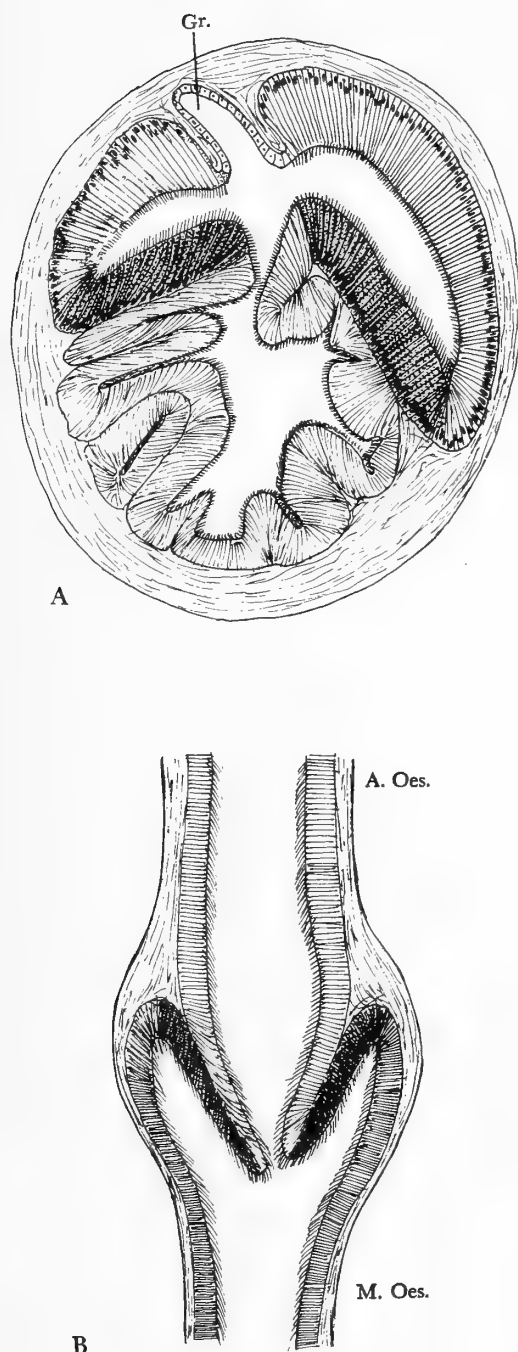


Figure 13

Provocator pulcher: valve of Leiblein; A, frontal section; B, transversal section A. Oes. - anterior oesophagus Gr. - non-ciliated groove M. Oes. - mid-oesophagus

When crossing the nerve ring, the mid-oesophagus has a diameter of about 1.5 mm. Its walls are thin. The muscular layer is very weak at its beginning, the fibers have the same disposition as in the anterior part. The external layer of circular muscle fibers is thicker. The inner epithelium forms a few low ridges. At a short distance from the beginning, the gland of Leiblein (Figure 11) begins with swellings that appear on the dorsal wall of the oesophagus. The gland is progressively differentiated as a tubular, elongate organ coiled upon itself in a compact mass surrounding the oesophagus. The lumen is alveolar with muscular compartments. The gland is composed of 3 distinct parts. The first is lined with tall columnar gland cells with few mucocytes; the muscular layer is very thin. In the next part, the wall has a thick muscular layer and bears longitudinal and transverse ridges. The glandular epithelium is composed of a higher percentage of mucocytes. The dead end of the gland forms a sac 2 to 2.5 mm wide. Its wall is very thin and lined in most of its parts by a flattened epithelium. There are a few scattered low ridges of gland cells comprising some mucocytes. The bad fixation of the tissues in this part of the digestive tract prevented better interpretation.

Unidentified food remnants have been found in this part of the alimentary canal. Behind the gland of Leiblein, the posterior part of the mid-oesophagus has a diameter of 1.9 mm; its internal wall bears many longitudinal ridges.

The posterior oesophagus is separated from the preceding part by a constriction. Its section increases rapidly to a diameter of 2 to 2.5 mm. The muscular layer is very thin, the epithelium consists of ciliated cells and mucocytes. There are digitated internal ridges.

The U-shaped stomach is a very simple sac with an internally plicated wall. The ridges of the dorsal part of the posterior oesophagus reach the single digestive gland aperture. The ventral ridges continue in the intestine without interruption.

The intestine runs from the stomach along the right pallial wall. Its diameter is 2 to 3 mm. The thin muscular layer is lined with an epithelium which is thickened into longitudinal ridges of columnar, ciliated gland cells with numerous dark granules. The mucocytes, scattered at the beginning, are much more abundant towards the end. The anal gland is a branching tubule derived from an invagination of the renal wall. Its cells are ciliated and granular.

Discussion: With these observations, it is possible to determine the systematic position of the genus *Provocator*. This genus has been classified in the subfamily Zidoninae by CLENCH & TURNER (1964) on the basis of the morpho-

logy of the radula. This placement is corroborated by the following observations:

- uniseriate radula with tricuspid teeth;
- accessory salivary glands loosely bound around moderately compact salivary glands;
- lobes at the bases of the siphon of equal development;
- absence of operculum.

It should be added that the genus *Provocator* could be considered more primitive than *Alcithoe* by the fact that its gland of Leiblein is less detached from the oesophageal wall than in the latter genus (compare the anatomical description of *Alcithoe arabica* by PONDER, 1971).

On the specific level, the very close similarity should be noted between the radular teeth of *Provocator pulcher* (Figure 12A) and *P. corderoi* (cf. plt. 107 in CLENCH & TURNER, 1964); the teeth of the latter species are somewhat more slender, with more arcuate bases.

Family Volutomitridae

Volutomitra curta (Strebel, 1908)

Paradmete curta STREBEL, 1908: 23, plt. 3, figs. 34a-e; POWELL, 1951: 166; CARCELLES, 1953: 196; POWELL, 1958: 198; 1960: 157

Paradmete longicauda STREBEL, 1908: 24, plt. 3, figs. 36a-b; POWELL, 1951: 165; CARCELLES, 1953: 196, plt. 3, fig. 70

Volutomitra (Paradmete) curta. CERNOHORSKY, 1970: 103, plt. 13, figs. 11-13

Specimens (all from Kerguelen Islands):

MD.03: 3-CP2, 6 (1); 3-DS1, 1; 6-CP3, 3; 17-CB5, 70 (9); 21-CP14, 1; 24-CB6, 2

MD.04: 15-DC37, 1; 17-DC39, 1; 24-DR58, 1 (2); 38-CP92, 1; 47-DC108, 1; 82-CP196, (1); 113-DC269, (1); 115-DC275, 1

Distribution: The type locality is Shag Rock Bank, 53° 34'S, 43° 23'W, 160 m, gravel and sand, bottom temperature +2.05°C. It was known from Shag Rock Bank,

South Georgia Island, Enderby Land, Mackenzie Sea. First recorded here (cf. Figure 7) from Kerguelen Islands, a major northward extension of range of this volutomitrid. Not obtained at Crozet Islands or Marion/Prince Edward Islands during our surveys.

Bathymetric Range: Was known living from 75 to 300 m. Thus it is of interest to point out that this species was obtained living off Kerguelen Islands from 120 m to as deep as 650 m (present material).

Ecology: Rather similar to that of *Volutomitra fragillima* (the 2 species are frequently collected together) but with a lower temperature-tolerance which would account for its absence from both the Crozet and Marion/Prince Edward shelves.

Anatomy (Figures 14, 15): Animal rather small; maximum height of the shell: 28.6 mm. Tentacles cylindrical, bearing eyes on their posterior side. Operculum present.

The Alimentary Canal:

The pleurembolic proboscis is relatively long. The wall of the proboscis sheet is transversely plicate. The strong retractor muscles connect its sides to the lateral walls of the body. The ventral wall of the buccal cavity is protected by a chitinous shield. The accessory salivary gland is an unpaired organ as in other Volutomitridae. This gland is quite small and entirely concealed in the proboscis. Its thin secretory duct lies just behind the chitinous shield of the buccal floor and opens at the mouth aperture. Histologically the gland consists of a tube lined with cubic epithelium, the cells possessing large nuclei, and an outer layer of circular muscle fibers. Few gland cells are situated in its terminal part. The radula is triseriate. The central tooth is quite large with a single thin lanceolate cusp and 2 long basal processes (Figure 12C). The lateral teeth are small and short.

The salivary glands are small; the secretory tubules are composed of one type of cell. The salivary ducts enter the wall of the oesophagus in front of the valve of Leiblein. They open into the buccal cavity close to the junction of

Explanation of Figures 1 to 6

Figure 1: *Provocator pulcher*, height 85 mm, from Kerguelen Islands, MD. 03-24-CB6

Figure 2: *Volutomitra curta*, height 15.6 mm, from Kerguelen Islands, MD. 03-17-CB5

Figure 3: *Volutomitra fragillima*, height 15.4 mm, from Kerguelen Islands, MD. 04-F51-DC119

Figure 4: Egg capsule of *Provocator pulcher* on a valve of *Malletia gigantea* measuring 47 × 28 mm; Kerguelen Islands, MD 04-H95-DC233

Figure 5: Two egg capsules of *Provocator pulcher* on an egg capsule of skate, Kerguelen Islands, MD. 03-21-CP14

Figure 6: The same capsules, enlarged

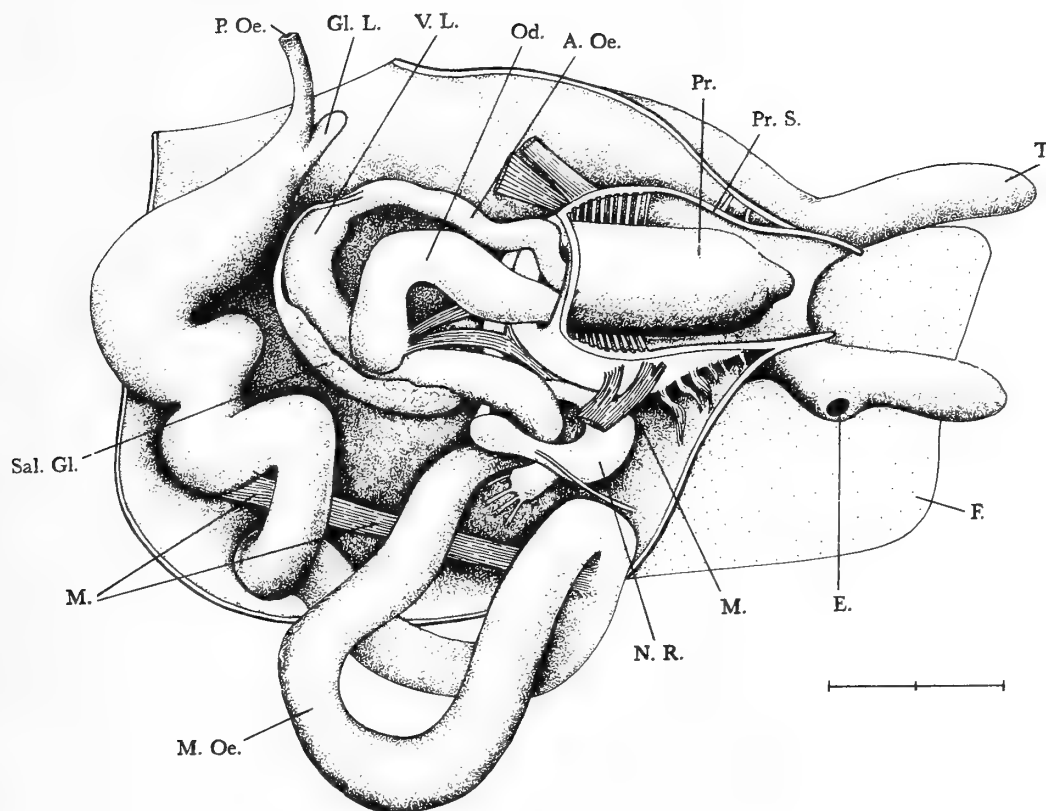


Figure 14

Volutomitra curta: anterior part of the digestive tract. Abbreviations as for Figure 11. E - eye M - muscular bundles

the oesophagus. The ducts are densely ciliated, the cilia having a forward orientation.

The anterior oesophagus is relatively narrow. There are 2 lateral ciliated ridges. Ventrally the epithelium is composed of flattened, nonciliated cells. Gland cells filled with red granules are in all this part of the digestive tract.

The mid-oesophagus begins with the valve of Leiblein. The tract is rather long and coiled upon itself, a strong muscular bundle is attached between 2 loops. The valve of Leiblein, situated well in front of the nerve ring, is quite typical. The ventral non-ciliated groove of the anterior oesophagus persists as a deep slit into the fold of the valve. This groove, ventral in the anterior part of the valve, moves progressively to the right and becomes dor-

sal posteriorly. This evidence of torsion thus occupies the same level as in the Volutidae. Two bundles of longitudinal muscle fibers are developed into the wall of the valve, below the ridges lining the non-ciliated groove. The histological organisation of the valve corresponds to the one observed in *Provocator*, except the 2 conspicuous muscular bundles present in its walls. The mid-oesophagus possesses a ciliated groove which corresponds to the pretorsional dorsal alimentary tract of the anterior oesophagus. At its beginning, the wall of the mid-oesophagus is thin; later on, it becomes thicker by increase of the internal layer of circular muscle fibers. The numerous mucocytes and the red-stained cells that constitute the dorsal epithelium of the first part of the mid-oesophagus are pro-

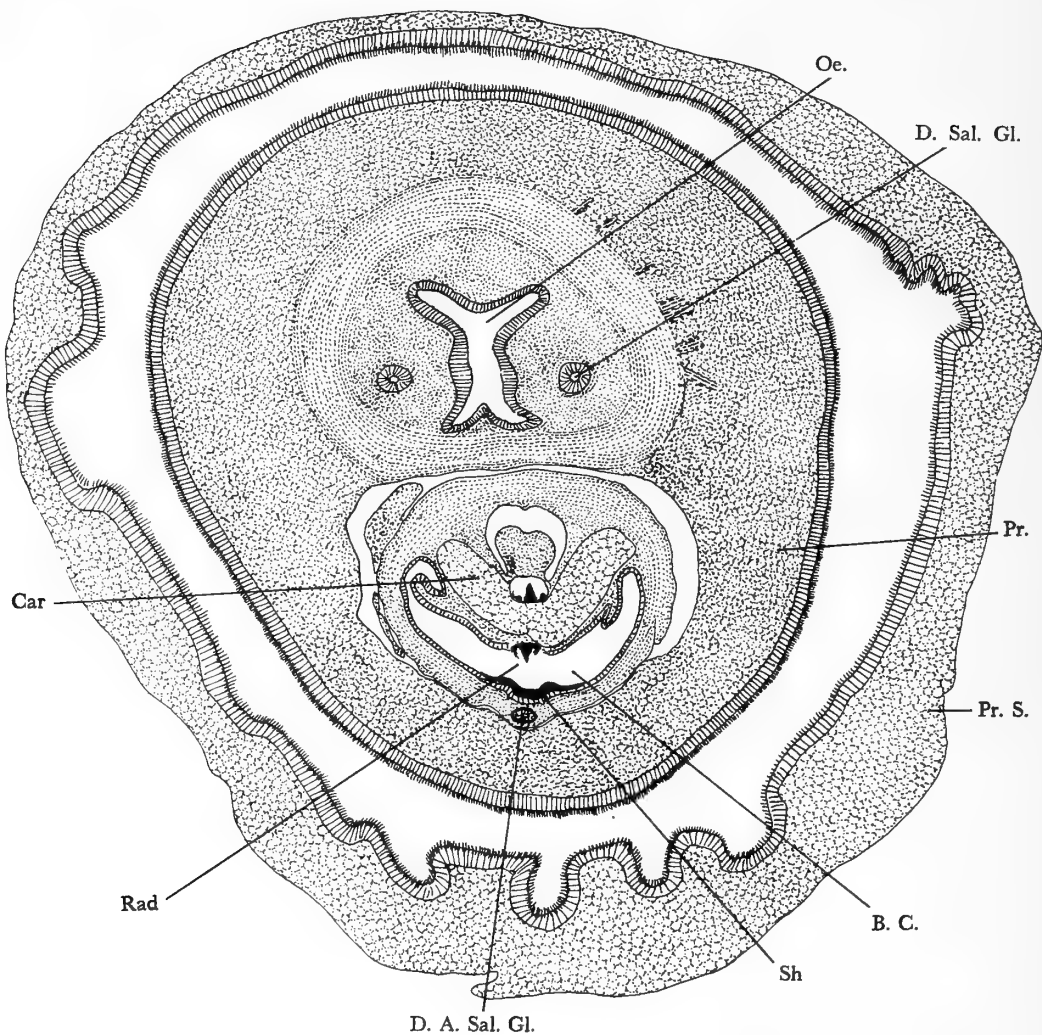


Figure 15

Volutomitra curta: transverse section through proboscis.

B. C. - buccal cavity Car. - subradular cartilage D. A. Sal. Gl. - common duct of accessory salivary glands Rad. - radula
Oe. - oesophagus Pr. - proboscis Pr. S. - proboscis sheet

gressively replaced by gland cells of irregular shape and filled with brown granules. These latter elements are restricted to the dorsal part of the lumen and are separated from the ventral ciliated groove by 2 low ciliated ridges. Further on the dorsal part is completely isolated and forms the gland of Leiblein. At its posterior end, the gland emerges out of the wall of the mid-oesophagus as a small

translucent vesicle. Its histology seems to be uniform.

The transition from the mid-oesophagus to the posterior oesophagus is visible externally as a rapid decrease in the external diameter of the duct. Nevertheless, the size of the lumen remains constant, as there is a considerable diminution of the muscular layers of the wall. The lumen is lined with ciliated epithelium.

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

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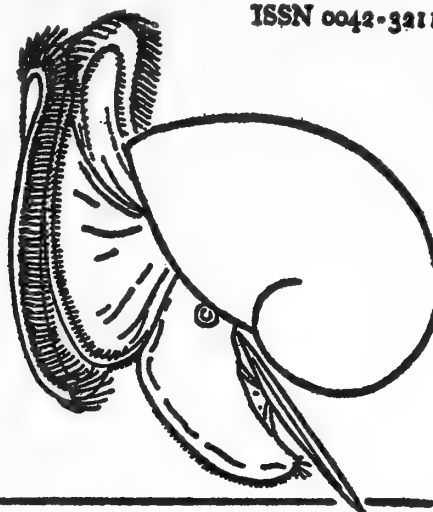
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

Egg Masses of Mollusca from Mediterranean Waters of Israel and Notes on Reproduction of the Freshwater Species

Theodoxus jordani and *Melanoides tuberculata*

BY

AL. BARASH AND Z. ZENZIPER

(14 Plates; 1 Text figure)

INTRODUCTION

A SERIES OF PAPERS on the molluscan fauna of the Mediterranean coasts of Israel has been published during the last decades. But only a few observations deal with the reproduction of Mollusca in this area (BARASH & DANIN, 1973; RAHAT, 1973). The purpose of the present work is to give a preliminary report on egg masses of marine molluscs found in the intertidal and infralittoral zones of the Mediterranean Israel and Sinai Peninsula. The Mediterranean coast, along which the material discussed here was collected, extends from Rosh-Haniqra in the North (Lebanon border) to Bardawil (Sinai Peninsula), near the northern entrance of the Suez Canal (see map).

Most egg masses were collected during field trips and expeditions, some were brought after months and even years of having been preserved in alcohol; accurate counting and measuring thus were often beyond our reach. In several cases, adult parent animals were put into aquaria, where they deposited their spawn, thus confirming the identity of the egg masses found in the sea. These included: *Cerithium scabridum*, *C. rupestre*, *Columbella rustica*, *Bulla striata*, *Aplysia fasciata*, *Bursatella leachi savigniana*, *Elysia timida*. The spawn of *Rhinoclavis kochi* was found only in the aquarium.

Egg masses were first sent for identification in 1966 to the late Professor Gunnar Thorson at the Zoological Museum of the University of Copenhagen. Unfortunately, his death interrupted his great scientific work and the material was returned to us containing identified egg masses of 6 species. Dr. Klaus Bandel, Friedrich-Wilhelms University, Bonn, identified egg masses of 5 species, and Dr. Nellie B. Eales, University of Reading, identified the egg masses of 2 species of Aplysiidae.

The greatest part of the material is kept in the collection of the Tel-Aviv University, Department of Zoology. The egg masses of *Cerithium rupestre* and *Elysia timida* are in the collection of the Hebrew University of Jerusalem, Department of Zoology.

The localities in which living adult specimens of the species treated in this paper were found are indicated; the vertical distribution of the species is also given. These data should be useful for future investigations of spawn of these species in the area.

LIST OF SPECIES CONSIDERED

GASTROPODA

PROSOBRANCHIA

MESOGASTROPODA

CERITHIIDAE

Cerithium scabridum Philippi, 1849

Cerithium rupestre Risso, 1826

Rhinoclavis kochi (Philippi, 1848)

JANTHINIDAE

Janthina ? nitens Menke, 1828

NATICIDAE

4 types, species not determined

CASSIDIDAE

Cassidaria echinophora (Linnaeus,
1758)

Semicassis undulata (Gmelin, 1791)

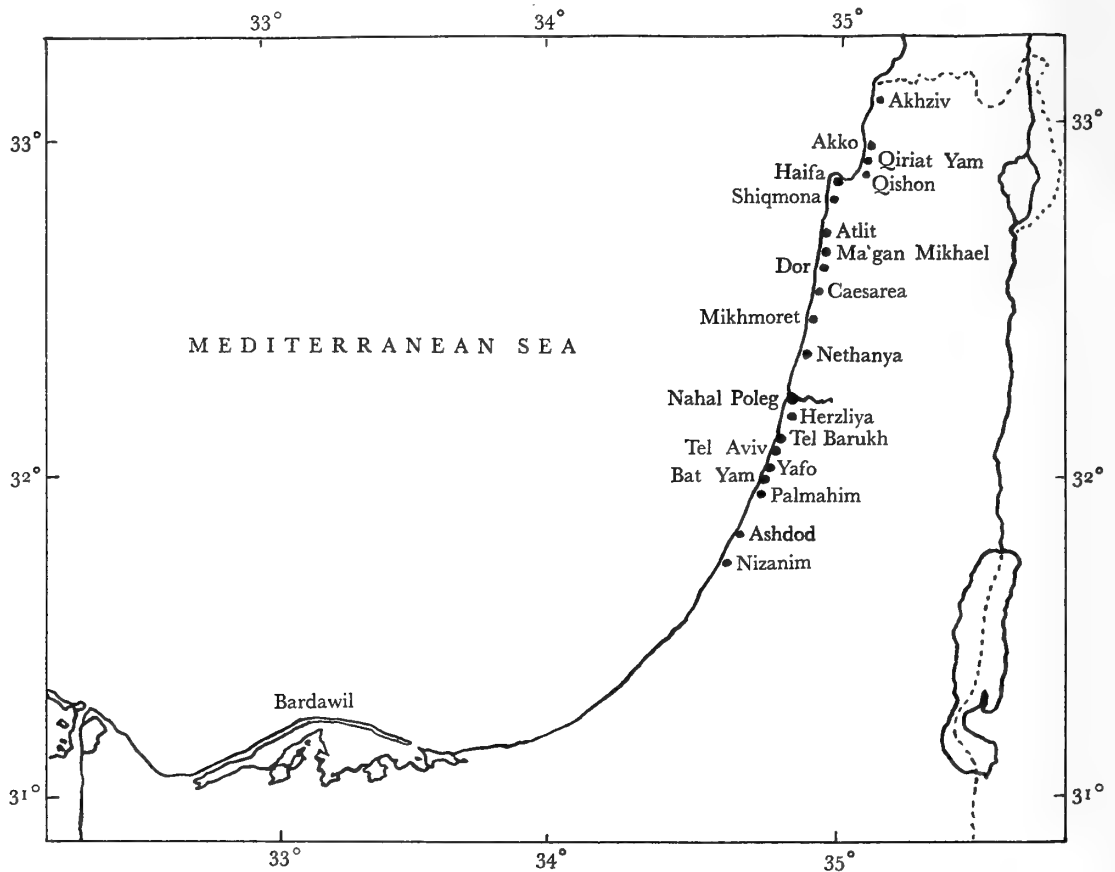


Figure 33

Collecting Localities of Molluscan Egg Masses at the Coasts of Israel and the Sinai Peninsula

TONNIDAE

Tonna galea (Linnaeus, 1758)

NEOGASTROPODA**MURICIDAE**

Trunculariopsis trunculus (Linnaeus, 1758)

Murex brandaris Linnaeus, 1758

THAIDIDAE

Thais haemastoma (Linnaeus, 1767)

Thais carinifera (Lamarck, 1822)

COLUMBELLIDAE

Columbella rustica (Linnaeus, 1758)

BUCCINIDAE

Euthria cornea (Linnaeus, 1758)

Pisania striata (Gmelin, 1791)

NASSARIIDAE

Sphaeronassa mutabilis (Linnaeus, 1758)

FASCIOLARIDAE

Fasciolaria lignaria (Linnaeus, 1758)

CONIDAE

Conus ventricosus Gmelin, 1791

OPISTHOBRANCHIA**CEPHALASPIDEA**

(Bullomorpha)

BULLIDAE

Bulla striata Bruguière, 1789

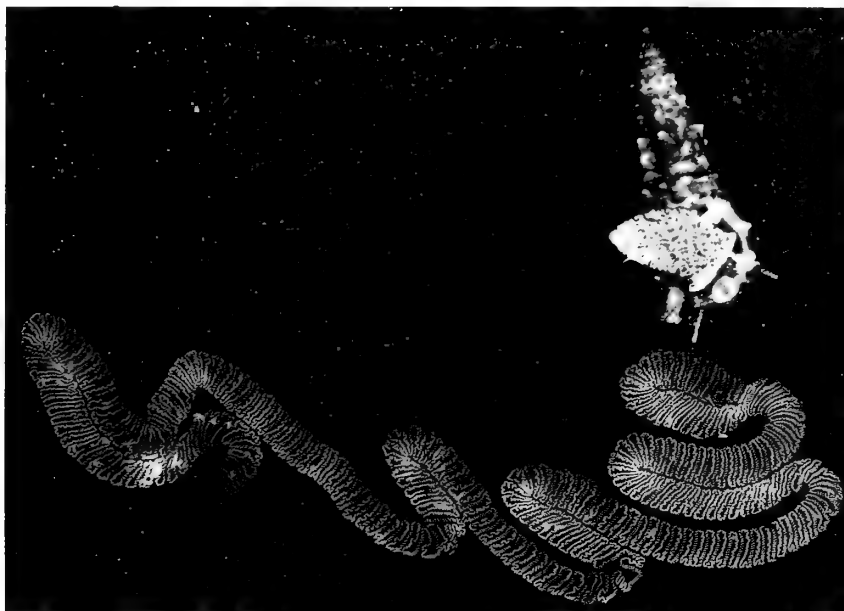


Figure 1

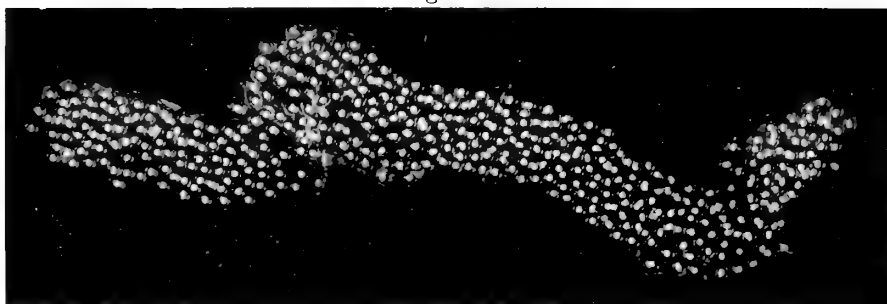


Figure 2



Figure 3

ANASPIDEA

(Aplysiomorpha)

APLYSIDAE

Aplysia fasciata Poiret, 1789*Bursatella leachi savigniana* Audouin,
1826

SACOGLOSSA

ELYSIDAE

Elysia timida (Risso, 1818)

NUDIBRANCHIA

GLOSSODORIDAE

? *Glossodoris* sp.

AEOLIDIDAE

? *Aeolidiella* sp.

CEPHALOPODA

DECAPODA

SEPIDAE

Sepia officinalis Linnaeus, 1758*Sepia elegans* d'Orbigny, 1826*Cerithium scabridum* Philippi, 1849

(Figure 1)

Records:

BARASH & DANIN, 1973: 309; fig. 7. Israel

AYAL, 1978: 114-115. Israel

Material:

Bat-Yam - 14. X. 1972; intertidal zone, attached to algae

Tel-Aviv University, aquarium: 3. X. 1972; 24. X. 1972; 25. X. 1972

Dor, Fisheries Research Station, aquarium: 15. XII. 1973

The egg masses of *Cerithium scabridum* were found fastened to solid objects (rocks, stones) in the habitat of the adults: rocky shores in the intertidal zone.

About 100 specimens of *Cerithium scabridum* were kept alive in the marine aquarium of Tel-Aviv University.

The snails were mostly attached to the vertical walls of the aquarium.

The first egg mass was observed on the glass wall of the aquarium on 3. X. 1972. The ribbon-like greyish egg mass consisted of opaque, irregularly coiled strings, 4 mm in diameter. The external limiting membrane of the string surrounds a thick gelatinous matrix in which egg capsules with transparent walls are embedded. Each capsule contains one egg (diameter 120 μ m). A string contains 5 000 to 20 000 eggs.

The string laid on 24. X. 1972 was transferred on the same day into a petri dish for closer examination. Many of the eggs were already divided in two; the following days, some of the capsules appeared darker and ciliary movement could be seen in them. On 30. X. 1972, veligers appeared, some within the string, enclosed in the thin transparent membrane of the capsule, but most were swimming freely in the dish. The veligers had a distinct shell. Remnants of the disintegrated strings floated in the water.

Cerithium scabridum is one of the earlier Indo-Pacific immigrants from the Red Sea into the Mediterranean. The first appearance on the Mediterranean coasts of Israel was recorded by PALLARY, 1912: 110; pl. 15. At present they are abundant there.

Distribution of adult animals along the Mediterranean coasts of Israel: Akhziv, Shave-Ziyyon, Nahariya, Akko, Qiryat Hayyim, Qishon, Atlit, Caesarea, Dor, Habonim, Mikhmoret, Netanya, Tel-Barukh, Tel-Aviv, Yafo, Bat-Yam, Ashdod, Bardawil.

Vertical Distribution: Intertidal zone.

Cerithium rupestre Risso, 1826

(Figure 2)

Record:

BANDEL, 1975: 91. Banyuls-sur-Mer

Material:

Specimens of *Cerithium rupestre* taken from Shiqmona were kept in an aquarium of the Hebrew University, Jerusalem.

The following data are based on the investigations of Dr. Y. AYAL (1978: 186-187). Spawn was observed in the aquarium during 1976; similar egg strings were deposited in September 1977. The number of eggs in a string varies between 100 and 700; the diameter of an egg is 400 μ m. Development is direct; the juveniles hatch after development of about 15-25 days after spawning.

According to the information on spawning of *Cerithium rupestre* at Banyuls-sur-Mer (BANDEL, 1975: 91),

the gelatinous strings of the spawn contain 70-100 eggs (?), from which the juveniles hatch after development of about 3 weeks, having already completed metamorphosis within the egg capsules.

Distribution of adult animals along the Mediterranean coast of Israel: Akhziv, Nahariyya, Shave-Ziyyon, Akko, Haifa, Bat-Gallim, Shiqmona, Atlit, Dor, Caesarea, Netanya, Herzliyya.

Vertical Distribution: Intertidal zone to 2 m depth, rocky shores.

Rhinoclavis kochi (Philippi, 1848)

[= *Cerithium kochi* Philippi, 1848]

(Figure 3)

Record:

BARASH & DANIN, 1977: 110; fig. 8. Israel.

Material:

Tel-Aviv University, aquarium, 28. III. 1975

Specimens of *Rhinoclavis kochi* taken from Haifa Bay were kept in the aquarium of Tel-Aviv University. On 28. III. 1975 Mr. M. Tom found coiled strings on the sandy bottom of the aquarium. The strings appeared brownish yellow because of the sand grains adhering to them. Minute, round vesicle-like capsules were observed by examination under the microscope. The egg capsules were embedded in a gelatinous matrix and were considerably smaller than the sand grains. Yolky eggs could be seen through the transparent wall of the capsules. Some of the eggs were in early cleavage stages (2 to 4 cells).

Distribution of adult animals along the Mediterranean coast of Israel: Nahariyya, Akko, Qiryat-Hayyim, Haifa Bay, Karmel Beach, Shiqmona, Atlit, Dor, Alexander River, Netanya, Tel-Barukh, Rubin River, Ashdod, Ashqelon, Nizanim, Yunis, Gaza.

Vertical Distribution: a) Intertidal zone – rare; b) mostly infralittoral, 10-101 m depth, sand, sandy mud.

Rhinoclavis kochi is one of the most successful Indo-Pacific immigrants from the Red Sea into the Mediterranean, and is at present abundant in the Mediterranean waters of Israel.

Janthina ? nitens Menke, 1828

(Figure 4)

Record:

FRAENKEL, 1927: 604-607; plt. III, figs. 1-4; text figs. 5-6

Material:

Tel-Aviv, 24. XII. 1944

A snail with the raft and spawn attached to it was found by a student during a field trip to the sea shore. The material preserved in 70% alcohol shrank considerably. Nevertheless, we were able to distinguish the shell of the adult, the soft body, the raft connected with the foot and the brown egg capsules attached to the raft.

The egg capsules are attached to the underside of the raft by a mucous string. They are pear-shaped, fixed on the string by their narrow end. Capsules in which veligers are swimming appear brown because of the larval brown shell seen through the transparent capsular wall (*vide* FRAENKEL, 1927).

The only egg mass of the pelagic *Janthina* was found in a condition which did not allow identification as to its specific affinity because of the shrunken shell preserved in alcohol for years. We surmise that of the 3 species of *Janthina* known in the Mediterranean malacofauna of Israel, this spawn belongs to *J. nitens* which is not uncommon on our coasts. Another oviparous species, *J. globosa* (*vide* ROBERTSON, 1974: 218-219) is represented in the collections of Israel by one shell only. The common species of *Janthina* in Israel, *J. bicolor*, is probably ovoviviparous; egg capsules of this species were never found attached to its floating raft.

NATICIDAE

The flat, coiled ribbon-like egg masses or "collars," encrusted with particles of the sea bottom, are easily recognized as belonging to Naticidae. The eggs are deposited in regularly arranged egg spaces, the spaces lacking exit holes (the larvae are released when the collar becomes brittle and crumbles).

Specimens of this family were not observed by the writers during spawning and thus were unable to refer the egg masses collected to definite species. They are divided here into 4 types according to the following characters: form of collar, number of whorls, particles of sea bottom, size of egg spaces and eggs.

Type A

(Figure 5)

Material:

Palmahim, 23. IV. 1977; cast ashore



Figure 4

Figure 5

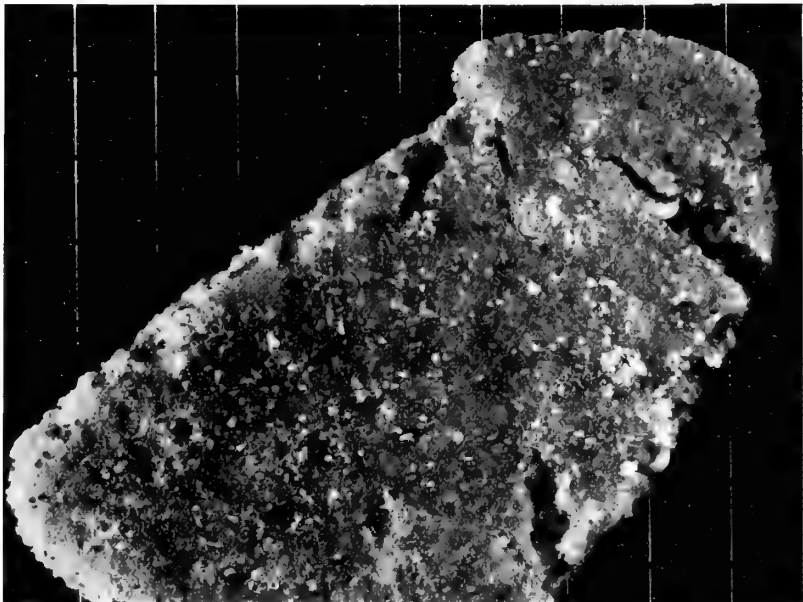


Figure 6a

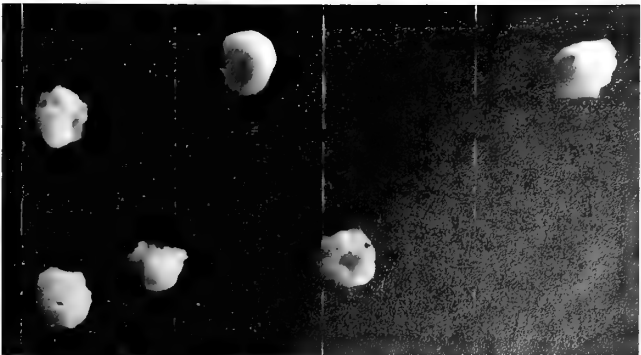


Figure 6b

The arched leathery, dark brown egg ribbon forms an almost complete "collar," encrusted with fine particles of sand and mud. Measurements of the collar: 9.2 cm periphery, 2 cm wide; 1.2 mm thick. The egg spaces are arranged in one plane with 25 spaces per $\frac{1}{4}$ cm²; each space contains one white oval egg ($125 \times 90 \mu\text{m}$).

Type B

(Figures 6a, 6b)

Material:

Akhziv: 22. IV. 1960; 23. IV. 1966
Qiryat Hayyim: 14. III. 1969
Haifa: 14. III. 1964; 11. V. 1969
Dor: 7. III. 1969
Tel-Barukh: 2. III. 1962

The brittle egg collars were collected in a fragmented state (no complete collars). The colour is grey-pinkish; the egg mass is 1.2 to 1.4 mm thick; the egg spaces are arranged in a single plane relatively widely apart, 9 spaces per $\frac{1}{4}$ cm². Each space contains one round, white-brownish egg ($110 \times 100 \mu\text{m}$).

Type C

(Figures 7a, 7b, 7c)

Material:

Haifa Bay: 29. IV. 1968; 14 m deep; 14. V. 1974;
24 m deep
Palmahim: 10. V. 1977; 20 m deep; 21. IV. 1977,
on beach
Nizanim: 12. IV. 1977; 20 m deep

Many parts of collars of different sizes and one complete collar were collected, mostly by dredge. The complete collar is 10.5 cm in periphery, 1.8 cm wide, 1.2 mm thick. The grey-brown ribbons of this type are encrusted

with coarse sand grains. The outer and inner edges of the ribbon lack egg spaces; the outer edge is slightly undulated, 4-5.5 mm broad; the inner edge is only 2.5-3 mm broad. The thin-walled egg spaces are densely arranged in a single plane, bulging from the surface; there are 25 egg spaces per $\frac{1}{4}$ cm². Each space contains one white round egg ($110 \times 100 \mu\text{m}$).

Type D

(Figures 8a, 8b, 8c)

Material:

Nizanim: 12. IV. 1977; 10. V. 1977
Palmahim: 10. V. 1977. Infralittoral zone, 20 m deep

The grey-brown collars were complete, 1.1 mm thick. Unlike the collars of other types, these are spirally twisted in 3 whorls. Similar to the ribbons of type C, the edges are lacking egg spaces and the outer edge is undulated.

The outer whorl of the collars measures:

7.2 cm periphery, 2 cm wide (Nizanim, 10. V. 1977)
6.5 cm periphery, 2 cm wide (Nizanim, 12. V. 1977)
11.0 cm periphery, 2.5 cm wide (Palmahim, 10. V. 1977)

The egg spaces are arranged in a single plane, 16 spaces per $\frac{1}{4}$ cm², each space contains a white, small oval egg ($90 \times 70 \mu\text{m}$).

The Naticidae are represented in the Israel Mediterranean by 9 species. Very common are: *Neverita josephina* Risso, 1826; *Naticarius millepunctatus* (Lamarck, 1822); *Tectonatica flammulata* (Requien, 1848). Fairly common is also *Naticarius dillwyni* (Payraudeau, 1826). The egg masses in our collection may probably be assigned among these species.

Type D of the egg masses of Naticidae seems to be similar to the egg masses of *Natica (Mamma) mamilla* Linnaeus described by GOHAR & EISAWY (1967: 114-115; figs. 1, 2) from Al-Ghardaga on the north-western coast

Measurements of the egg masses of four types of Naticidae

Type	Ribbon		Egg spaces		Eggs		
	thickness	granules	density ⁴	cross section	colour	form	size
A	1.2 mm	10 μm	25	$0.8 \times 0.7 \text{ mm}$	white	oval	$125 \times 90 \mu\text{m}$
B	1.2-1.4 mm	25 μm	9	$0.8 \times 0.9 \text{ mm}$	white-brown	rounded	$110 \times 100 \mu\text{m}$
C	1.2 mm	25 μm	25	$0.9 \times 1.0 \text{ mm}$	white	rounded	$110 \times 100 \mu\text{m}$
D	1.1 mm	20 μm	16	$0.8 \times 0.7 \text{ mm}$	white	oval	$90 \times 70 \mu\text{m}$

(for Plate Explanations see foldout at page 317)

of the Red Sea. However, to our knowledge, *N. mamilla* was not mentioned so far among immigrants from the Red Sea into the Mediterranean (BARASH & DANIN, 1973, 1977).

Cassidaria echinophora (Linnaeus, 1758)

(Figures 9a, 9b, 9c)

Records:

LAMY, 1928: 114

FIORONI, 1966b: 684-688; Banyuls-sur-Mer; 60-80 m depth

Material:

[det. Klaus Bandel]

Caesarea - 21. III. 1962; one egg mass

Mikhmoret - 27. III. 1962; 3 egg masses

Ashdod - 8. VI. 1971; 1 egg mass

The egg masses were found in the intertidal zone. They consist of cup-shaped capsules connected by a dense jelly-like substance, forming irregular clusters. The number of capsules per cluster ranges from 4 to 75. The roundish capsules, 4 mm high, contain numerous eggs visible through the translucent walls.

"The capsules have no preformed escape aperture. Thus, the hatching snails are forced to burst a hole, fairly large, in the wall. Out of 155-193 eggs in a capsule only 7-23 young develop. ... The juveniles hatch in crawling stage." (FIORONI, 1966b: 684, 839)

Distribution of adult animals along the Mediterranean of Israel: Qiryat-Hayyim, Haifa, Shiqmona, Karmel Beach, Atlit, Dor, Caesarea, Hadera, Tel-Barukh, Tel-Aviv, Rubin River, Palmahim, Ashdod, Ashqelon, Gaza, Yunis, Tel-Arish, Bardawil.

Vertical Distribution: Infralittoral, 22-220 m depth, sandy mud, mud.

Semicassis undulata (Gmelin, 1791)

[Synonym: *Cassis sulcosa* (Brugière, 1792)]

(Figure 10)

Record:

LAMY, 1928: 114, *Cassis sulcosa* (Brug.)

Material:

[det. Klaus Bandel]

Dor - 17. VIII. 1969, 1 egg mass, depth unknown

Haifa Bay - 11. VI. 1975, 1 egg mass, depth 32 m

Palmahim - 29. VI. 1977, 3 egg masses, depth 20 m

The egg mass of *Semicassis undulata* is a tower-like structure composed of pillar-like capsules arranged one above the other in regular layers. Each capsule is about 8 mm high, the walls are semi-transparent and numerous yellowish eggs are seen within the capsules.

The spawn dredged at Palmahim (29. VI. 1977) constitutes a block containing 3 egg masses. The largest comprises 13 layers. The height of this egg mass is 6.5 cm, the width 5 cm at its lower end (which is attached to an alga), and 3.5 cm at the free upper end. Two smaller egg masses adhere to the large egg mass at right angles; one of them consists of 3 layers of capsules, the other of 4.

Distribution of adult animals along the Mediterranean coasts of Israel: Nahariyya, Qiryat-Hayyim, Haifa Bay, Karmel Beach, Shiqmona, Atlit, Habonim, Caesarea, Maagan Mikhael, Hadera, Netanya, Herzliyya, Tel-Barukh, Bat-Yam, Palmahim, Ashqelon, off Bardawil.

Vertical Distribution: Infralittoral, 1.5-7 m depth (live); 22-82 m depth (shells).

Tonna ? galea (Linnaeus, 1758)

[= *Dolium ? galea* (Linnaeus, 1758)]

(Figure 11)

Records:

LO BIANCO, 1909: 635

LAMY, 1928: 115

Material:

[det. Klaus Bandel]

Turkey (Mediterranean coast) - 4. VIII. 1958, 1 egg mass, spaces with eggs

Qishon - 14. III. 1964, 1 egg mass, honeycomb-like, egg spaces empty

Dor - 15. VIII. 1971, 1 egg mass, spaces with eggs

The egg masses form sheets of considerable size (up to 24 cm long). It was impossible for us to state with certainty the size of the sheets since they were torn into strips (the measurements given below are approximate). The eggs are within spaces in the gelatinous matrix of the sheet, which is yellowish (Turkey) or pinkish (Dor). The oval, angulate (quadrilateral to hexagonal) spaces are regularly arranged in rows in a single plane. The spaces are clearly separated one from the other, their walls semi-trans-



Figure 7 a

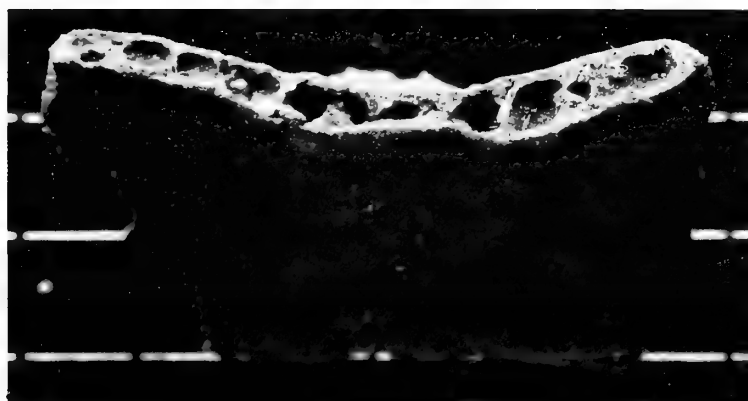


Figure 7 b

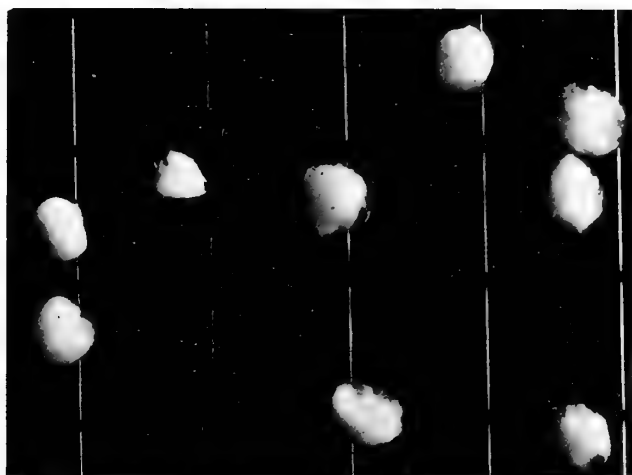


Figure 7 c

parent', numerous eggs are visible in the spaces, even in preserved material. According to THORSON (1940: 192), there are 20-40 eggs in a space. Each space has a pre-formed exit-hole on the outer surface of the sheet.

Egg mass	Length (max.)	Thickness	Dimensions of egg spaces	Egg spaces per cm ²
Turkey	24 cm	2.0 mm	2.5 × 2.0 mm	12
Israel: Qishon	4 cm	1.4 mm	1.0 × 0.8 mm	28
Dor	10 cm	1.6 mm	1.5 × 1.0 mm	16

It is worth quoting the remark of Dr. Bandel (personal communication, May 1977): "The sample of Turkey is quite like that of *Tonna galea* I have found in the Caribbean Sea. . . . The size of the capsules (spaces) is more dependent on the size of the producing female than on the species of the genus, therefore the three samples may be of the same species."

Egg masses of Tonnidae (*Tonna galea*) show great similarity to those of Naticidae, but without (sand) encrustation. They form extensive sheets, the egg spaces are considerably larger than those of Naticidae, easily discerned on the surface.

Dr. Bandel, who examined our material of Tonnidae, could not establish with certainty the identity of the species to which the egg masses in our collection (Turkey, Israel) belong. Since "they are quite like that of *Tonna perdix* (OSTERGAARD, 1950), *Dolium costatum* (KNUDSEN, 1940) and *Dolium olearum* (GOHAR & EISAWY, 1967) - all show more or less the same type of spawn" (personal communication, 1977).

The common and almost only species of Tonnidae in the eastern Mediterranean (and in the Mediterranean in general) is *Tonna galea* (*Dolium crosseanum* is extremely rare), the egg masses treated in this paper obviously belong to this species.

Trunculariopsis trunculus (Linnaeus, 1758)

[= *Murex trunculus* Linnaeus, 1758]

(Figures 12a, 12b, 12c, 12d)

Records:

FISHER, P. H. & A. RAFFY, 1933: 1-4; figs. 1, 2. Banyuls-sur-Mer, and Endoume

¹ KNUDSEN (1950: 98) on *Dolium costatum*: "The wall of the egg spaces consists of two layers - an external gelatinous, transparent layer 0.2 - 0.3 mm thick, which goes without any interruption from one egg space into the other, and an internal hyaline covering the inside of the egg space."

BANDEL, K. 1975: 94-95, in aquarium, Banyuls-sur-Mer

FIORONI, P. 1966b: 688, table 2, Banyuls-sur-Mer, to ca. 10 m depth and in aquarium

Material:

Dor - 1. VI. 1965; 27. V. 1966; 12. V. 1969

Nahal Poleg - 26. VI. 1976

Herzliyya - 22. I. 1965; 5. VI. 1976; 19. VII. 1976

Tel-Aviv - 6. VII. 1965; 30. VI. 1976

Tel-Barukh - 27. VI. 1970; 6. V. 1977; 17. VI. 1977;

2. VIII. 1977; 21. X. 1977

Cyprus - 22. VIII. 1970

Egg masses cast ashore (apparently laid in shallow water) are commonly found all year round; according to our observations they are especially abundant in May-July.

The egg masses of *Trunculariopsis trunculus* were regularly collected during 1976 by Z. Zensiper at Tel-Barukh, on the shore; measurements of these egg masses are as shown in small table at top of page 306.

The egg capsules are closely attached to each other by their rather broad, branched base and form irregular clusters of several layers. When freshly deposited, their colour is horny and slightly transparent; they become pale yellowish and less transparent later. The capsule is tongue-shaped, 5-6 mm high and 4-4.5 mm wide. One side of the capsule is convex with longitudinal ridges on its pergameneous wall. The other, the concave side, has a longitudinal depression where the escape aperture is found. Before hatching it is covered by a thin membrane.

Hatching does not seem to be simultaneous and the same cluster contains full as well as empty capsules. In a cluster collected on 12 May 1976, 38 out of about 400 capsules were empty with distinct open escape apertures. In another cluster collected 2 weeks later, 89 out of about 300 capsules were empty; it is worth noting that a few of them were with ruptured walls and covered escape aperture.

The egg mass collected in Cyprus contained juveniles before hatching. In the smooth brown embryonic shell the 2 last whorls and the siphonal canal were clearly seen (see Figure 12d).

Date	Clusters	Length	Width	Height
12. V. 1976	23	16.0-7.8 cm	11.2-6.0 cm	6.0-3.2 cm
5. VI. 1976	15	9.1-7.5 cm	6.1-5.2 cm	5.5-3.0 cm
12. VI. 1976	2	8.2-3.6 cm	7.2-2.5 cm	3.4-2.1 cm
19. VI. 1976	8	4.5-2.5 cm	3.1-2.4 cm	4.8-3.7 cm
26. VI. 1976	6	9.1-2.0 cm	5.0-3.2 cm	3.0-0.6 cm
30. VI. 1976	4	4.8-4.1 cm	3.5-2.7 cm	1.8-1.3 cm
12. VIII. 1976	1	3.5 cm	2.1 cm	1.4 cm

NOTE ON OVIPOSITION OF *Trunculariopsis trunculus*

"Many females participate in forming the egg mass, so that the bulk of the egg mass comprises many hundreds of capsules. From each capsule, after about a month of development, hatch at the average 15 young snails, which absorbed during their development 20-40 eggs. The juveniles leave their egg capsules in crawling stage, their metamorphosis was accomplished within the capsule." (BANDEL, 1975: 94).

Distribution of adult animals along the Mediterranean coasts of Israel: *Trunculariopsis trunculus* is common along the Israeli coasts, both in the intertidal and infratidal zones, from shallow waters to a depth of 84 m. They are found mostly on soft substrates: sand, sandy mud, mud, and less on rocks.

Intertidal zone (to 5 m depth): Akhziv, Nahariyya, Akko, Qiryat-Hayyim, Bat-Gallim, Shiqmona, Dor, Caesarea, Mikhmoret, Netanya, Herzliyya, Tel-Barukh, Tel-Aviv, Ashdod.

Infralittoral zone (dredged from 15-84 m depths): Caesarea, Dor, Qiryat-Hayyim, Haifa Bay, Atlit, Bat-Yam, Alexander River, Rubin River, Gaza, Bardawil.

Murex brandaris Linnaeus, 1758

(Figures 13a, 13b, 13c)

Record:

Lo BIANCO, 1909: 638. Naples

Material:

[det. Gunnar Thorson]

The egg masses of *Murex brandaris* form irregular clusters of various size (2-15 cm in diameter in our collection). The clusters comprise 20-300 cup-shaped, tough walled capsules. Each capsule is connected by a wide (1-2 mm) membranous extension of the wall to 2 or more neighbouring capsules. The measurements of the larger capsules are approximately 3 mm high, 4 mm wide; the smaller are 2.5 mm high, 2.8-3.0 mm wide. The exterior side of each capsule is convex, the interior concave. In the centre of the concave side a round exit hole is clearly seen. Through the semi-transparent capsule wall yellowish eggs are visible in fresh spawn. The egg capsules dredged in Palmahim contained shelled veligers (4-9) before hatching, in the crawling stage.

The clusters of *Murex brandaris* are smaller than those of *Trunculariopsis trunculus* and are found rarely, though adult specimens of *M. brandaris* are very common, as common as *T. trunculus*. The scarcity of egg masses of *M. brandaris* was confirmed by the late Professor Gunnar Thorson (personal communication).

Distribution of adult animals along the Mediterranean coasts of Israel: Akko, Haifa Bay, Dor, Zikhron Yaaqov, Caesarea, Alexander River, Tel-Aviv, Bardawil.

In the dredge haul of Dor along with the spawn 11 living specimens of *Murex brandaris* were found.

Vertical Distribution: Infralittoral zone, on sandy mud, sand, rarely on rocks or stones; at depths from 9-91 m.

Thais haemastoma (Linnaeus, 1767)

(Figure 14)

Records:

BARASH & DANIN, 1973: fig. 11. Israel

Localities	Date	Depth	Egg masses	Capsules	
				number	content
Haifa Bay	10. VII. 1974	73 m	2	60	many empty
Dor	6. V. 1968	64 m	1	73	with eggs
Tel-Barukh	VII. 1965	on rocky shore	1	70	mostly empty
Tel-Aviv	6. VII. 1945	on rocky shore	1	about 200	mostly empty
Palmahim	29. VI. 1977	80 m	1	250-300	with veligers

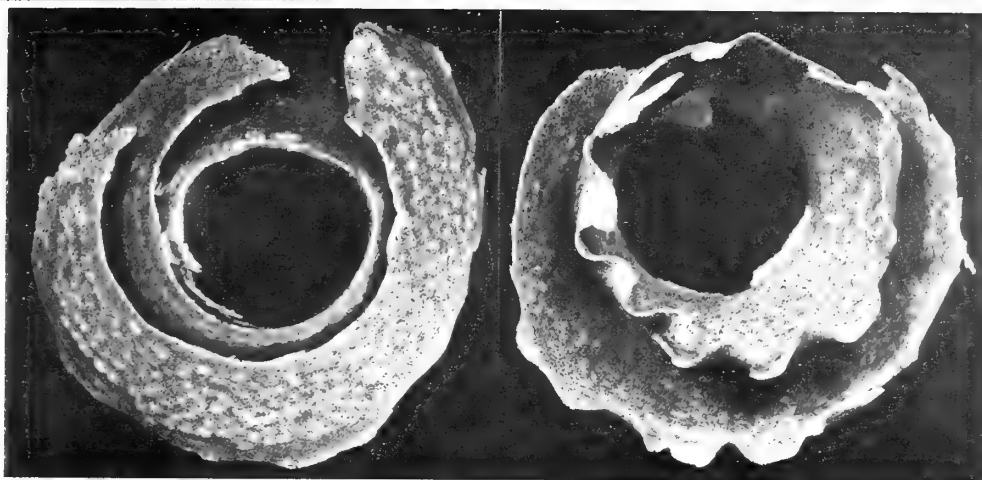


Figure 8a

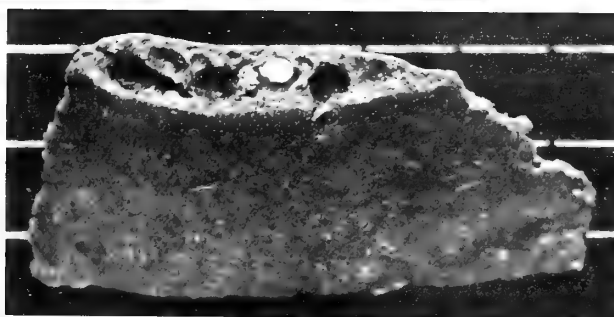


Figure 8b



Figure 8c

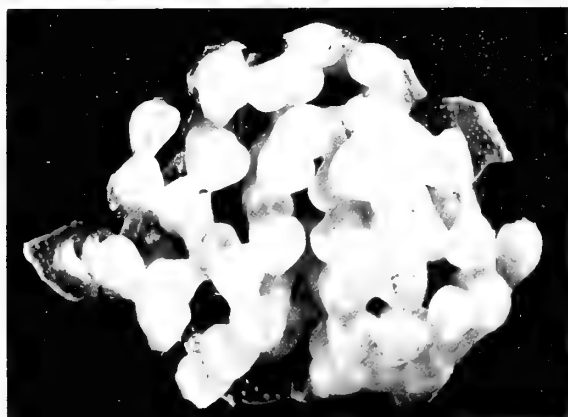


Figure 9a



Figure 9b

BANDEL, 1976b: 18. Santa Marta, Colombia, aquarium

Material:

Tel-Aviv: 6. VIII. 1957, 56 capsules; 8. VIII. 1957, 131 capsules; 2. VI. 1971, 85 capsules; intertidal zone

The egg masses of *Thais haemastoma* consist of capsules laid in groups of 56 - 131. The parchment-like semi-transparent walls of the capsules are white, pink or purple. The freshly laid capsules are white, becoming yellow or pink afterwards and purple before hatching of the veliger.

The capsules are fixed to a solid substrate (shells, algae), their flattened bases are confluent and have a common base for the group. They are elongated, pillar-like, narrowed at the base, broader at the top, 5-12 mm high, with one side slightly concave. They stand erect side by side, the concave side of one capsule turned toward the convex side of its neighbour.

The upper side of the capsule is flattened and almost semi-circular, surrounded by a pale narrow rim. A preformed round exit hole, covered with a transparent membrane, is situated slightly off centre on the upper side. The young leave through the preformed exit hole on the top when the membrane falls off.

Distribution of adult animals along the Mediterranean coasts of Israel: Akhziv, Nahariyya, Akko, Qishon, Qiryat-Hayyim, Haifa, Bat-Gallim, Shiqmona, Habonim, Dor, Caesarea, Maagan Mikhael, Mikhmoret, Netanya, Arshaf, Herzliyya, Tel-Barukh, Tel-Aviv, Yafo, Bat-Yam, Palmahim, Ashdod, Yunis, Rafah.

Vertical Distribution: Intertidal zone up to 4-9 m depth.

Thais carinifera (Lamarck, 1822)

(Figure 14)

Records:

THORSON, 1940: 202; fig. 19. Iranian Gulf
BARASH & DANIN, 1973: 313; fig. 10. Israel

Material:

[det. Gunnar Thorson]
Tel-Aviv - 18. VIII. 1961; 21. XI. 1961; 16. VIII. 1965; intertidal zone

The egg mass of *Thais carinifera* consists of a group of yellowish, pink or purple capsules with parchment-like, semi-transparent walls. The different colours of the cap-

sules are due to the stages of the embryos inside them, just as in *T. haemastoma*.

The capsules are fixed to a solid substrate (rock, algae, shell). They stand erect side by side, the broadened bases confluent. In large groups some of the capsules laid earlier may serve as a substratum, thus forming the first step towards an egg cluster (THORSON, 1940). The groups of capsules are of various sizes: the smallest consists of 15 capsules, the largest of about 180 (in our material). The cylindrical falciform capsules are slightly curved, narrowed at the top, where the exit hole is situated. The capsules are 8-11.5 mm high; their diameter near the top is 1.5-2 mm.

"In this species 95-280 eggs of 0.2-0.22 mm in diameter are found in one capsule, all developing into embryos (no nurse eggs). . . . Their size and well developed velum prove that the larva, when hatched will pass through a pelagic stage." (THORSON, 1940: 204)

Distribution of adult animals along the Mediterranean coasts of Israel: Akko, Qiryat-Hayyim, Karmel Beach, Shiqmona, Dor, Atlit, Herzliyya, Tel-Barukh, Tel-Aviv, Bat-Yam, Ashdod, Ashqelon, Yunis, Gaza, Bardawil.

Vertical Distribution: Intertidal and infralittoral zones 9-26 m depth.

Thais carinifera is an Indo-Pacific immigrant into the Mediterranean Sea and is now a resident in Israeli waters.

Columbella rustica (Linnaeus, 1758)

(Figure 15)

Records:

BACCI, 1947: 75-79; fig. 1. Naples
KNUDSEN, 1950: 106-107; fig. 15. Cape Verde Isl.
BANDEL, 1975: 100. Banyuls-sur-Mer

Material:

[det. Gunnar Thorson]
Bat-Yam - 1. VIII. 1964, 7 capsules; VIII. 1969, 2 capsules; 15. VII. 1976, 43 capsules

The egg masses were collected in the intertidal zone attached to algae, e. g., *Caulerpa*, *Pterocladia*.

The egg masses of *Columbella rustica* consist of oval, boat-shaped (turned upside down) capsules laid singly and attached to the substrate by their flattened base one by one, often in groups of 2 to 11 capsules. The capsule is 3 mm long and 2 mm high. The walls are transparent with numerous small ridges and fine striae forming a net-like pattern. An oval exit hole, 1 mm long, is situated

on the top of the capsule, its thickened edges forming a rim. The exit hole is conspicuous in empty capsules. The eggs are greenish with an average diameter of 160-180 μ m. Some capsules contained 2-19 embryos (which ingested during their development many nurse eggs); in 2 capsules a single large embryo with distinct shell was distinguished. "The juveniles escape after development lasting over 4 weeks in crawling stage. They accomplish the metamorphosis within the capsule long before hatching." (BANDEL, 1975)

Distribution of adult animals along the Mediterranean coasts of Israel: The adult animals live on rocks, usually among algae; adult specimens were collected in the following places:

Intertidal zone: Akhziv, Akko, Bat-Gallim, Habonim, Dor, Caesarea, Mikhmoret, Netanya, Arshaf, Tel-Barukh, Bat-Yam. — Infralittoral zone: Haifa Bay, Akko, Dor, Alexander River — at a depth of 18-37 m, on rocks and sandy mud substrate.

Euthria cornea (Linnaeus, 1758)

(Figure 16)

Records:

LO BIANCO, 1909: 636. Naples

LAMY, 1928: 53

BANDEL, 1975: 104. Banyuls-sur-Mer

Material:

[det. Gunnar Thorson]

Akhziv — 21. VI. 1956; intertidal zone, 95 capsules with eggs, 11 empty

Haifa — 13. II. 1965, ? , 9 capsules with veligers

Haifa — 11. VII. 1974, 74 m deep, 20 capsules, most with eggs

The eggs of *Euthria cornea* are laid in capsules arranged in several layers and united by their membranous extensions to clusters. The vase-like capsules are slightly flattened; their dimensions are: 4-5 mm long, 3.5-4.5 mm wide, narrowed at the base to 2.5 mm. The walls are semi-transparent, pergameneous. The number of eggs in each capsule varies from 8 to 22. All eggs will develop and hatch as veliconcha. — "The predatory *E. cornea* secretes in summer (June-July) an egg mass containing about 60 capsules similar to that of *Murex*. The spawn is composed of capsules containing 10-20 reddish eggs. After a development of over 3 weeks the juveniles that have just accomplished their metamorphosis escape." (BANDEL, 1975: 104).

Distribution of adult animals along the Mediterranean coasts of Israel: Akhziv, Nahariyya, Akko, Bat-Gallim, Haifa Bay, Shiqmona, Dor, Atlit, Caesarea, Maagan Mikhael, Alexander River, Tel-Aviv, Rubin River, Palmahim, Ashqelon, Gaza, Yunis, Bardawil.

Vertical Distribution: 1-70 m deep; sandy mud; mud

Pisania striata (Gmelin, 1791)

[= *Pisania maculosa* (Lamarck, 1822)]

(Figure 17)

Records:

FIORONI, 1966b: 701-704, tab. II. Banyuls-sur-Mer, to 2 m depth

BANDEL, 1975: 101. Banyuls-sur-Mer

Material:

[det. Klaus Bandel]

Akhziv — 14. V. 1971; intertidal zone, 4 capsules

Akko — 16. VI. 1975; 1-2 m deep on *Petricola lithophaga*, 5 capsules

The cup-like capsule, 3-4 mm in diameter, is flattened with a short peduncle at the base and a round exit hole on the upper side. In 3 capsules numerous small eggs could be seen; the others were filled with embryos. "The capsules contain 488-729 eggs of which 5-16 (extreme cases 24) develop" (FIORONI, 1966). The juveniles hatch in crawling stage.

Distribution of adult animals along the Mediterranean coast of Israel: Akhziv, Akko, Bat-Gallim, Shiqmona, Dor, Atlit, Caesarea, Habonim, Mikhmoret, Netanya, Arshaf, Tel-Barukh, Bat-Yam, Palmahim, Asqelon.

Individuals of *Pisania striata* dwell on rocks and stones in the intertidal zone to 1-2 m depths.

Sphaeronassa mutabilis (Linnaeus, 1758)

[= *Nassa mutabilis* (Linnaeus, 1758)]

(Figures 18a, 18b)

Records:

LO BIANCO, 1909: 639. Naples

LAMY, 1928: 92

FIORONI, 1965a: 544

Material:

[det. Gunnar Thorson]

Off Haifa — 29. IV. 1968; dredged, 109 capsules on *Cymodocea*, in 18-27 m

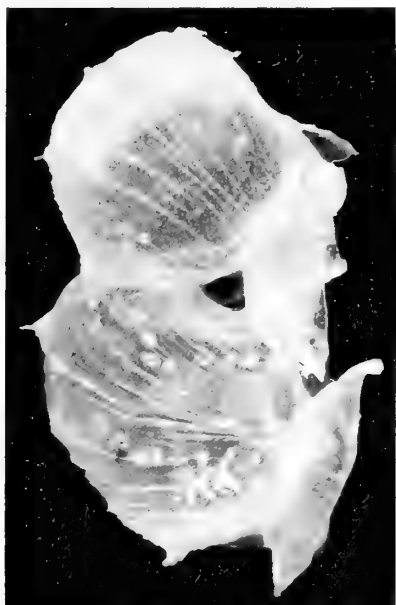


Figure 9c

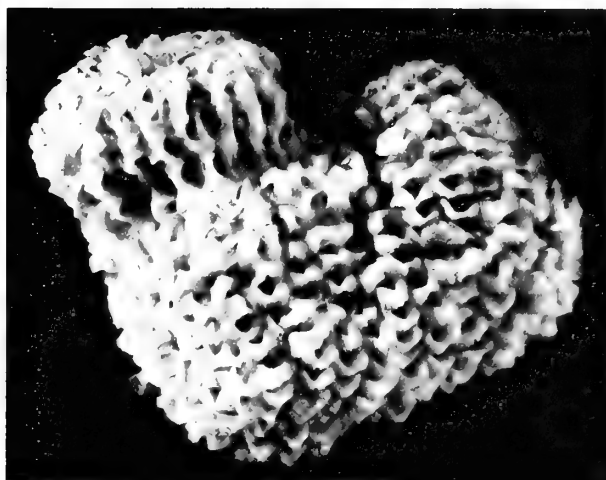


Figure 10

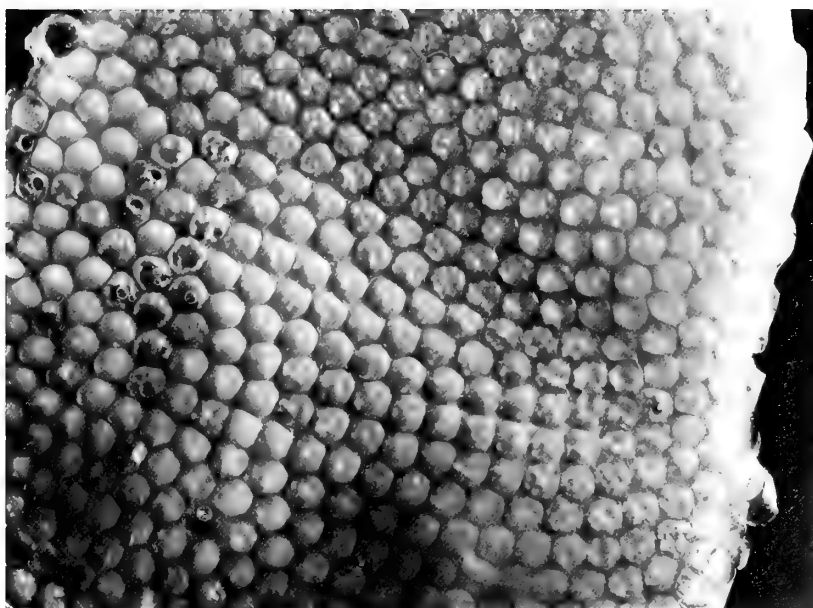


Figure 11

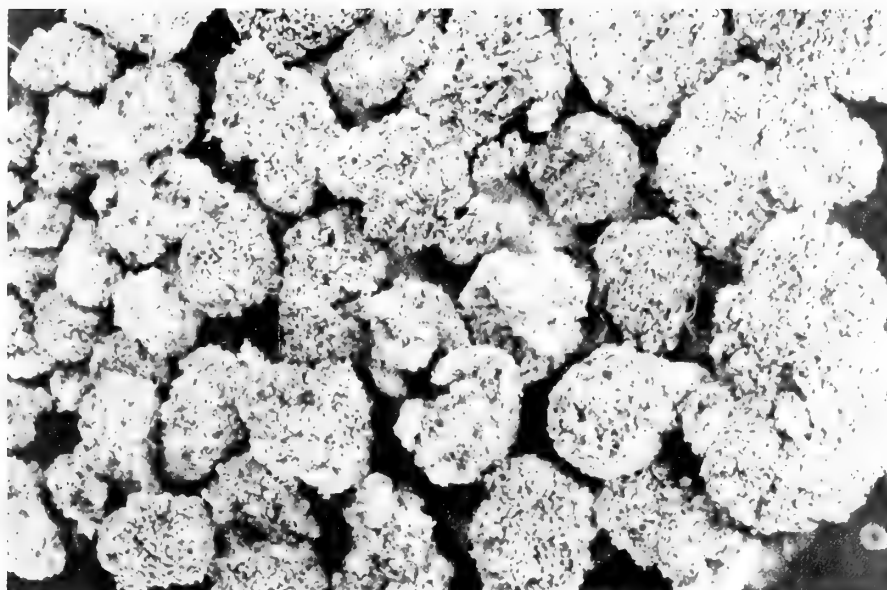


Figure 12 a



Figure 12 b



Figure 12 c

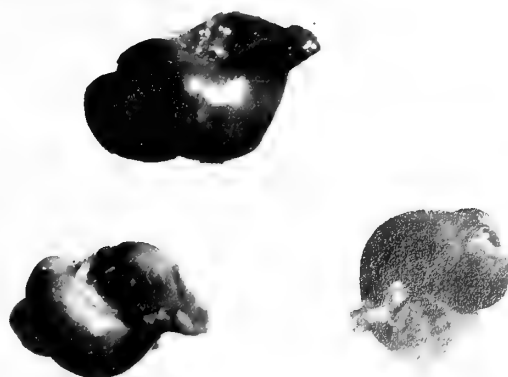


Figure 12 d

Atlit - 15. V. 1962; intertidal zone, 10 capsules on algae

Tel-Aviv - 28. II. 1963, 7 capsules on *Caulerpa*, washed ashore

Yafo* - 14. IV. 1963. Intertidal zone, 17 capsules on *Padina*

The flattened (antero-posteriorly compressed pouch-like capsules are fixed slightly obliquely to the substrate by their bases. They are arranged side by side in a line with equal spaces between them. The horn-coloured walls are semi-transparent with minute pleats on the surface. Each capsule of 3.5-4 mm height is narrowed at the top with thin undulated projections there.

The egg masses usually comprise 7-17 capsules; the egg mass from Haifa consisted of 109 capsules on the same plant (presumably egg masses laid by several individuals).

"The eggs are more or less rich of yolk, swimming in protein fluid within the capsule. The absorption of protein enables the hatching of veliconcha." (FIORONI, 1966: 655)

Distribution of adult animals along the Mediterranean coasts of Israel: Nahariyya, Akko, Qishon, Haifa, Atlit, Dor, Caesarea, Habonim, Alexander River, Netanya, Arshaf, Tel-Barukh, Tel-Aviv, Yafo, Bat-Yam, Palmahim, Ashdod, Nizanim, Gaza, Yunis, El Arish, Rafah, Bardawil.

Vertical Distribution: 8-88 m depths, sand, sandy mud, mud.

* The egg mass collected at Yafo seems to be of another nassariid species (see Figure 19)

Fasciolaria lignaria (Linnaeus, 1758)

(Figures 20a, 20b)

Records:

BACCI, 1947: 79-80; fig. 2. Naples (aquarium)

LAMY, 1928: 43

LO BIANCO, 1909: 636. Naples

Material:

[det. Gunnar Thorson]

The egg masses of *Fasciolaria lignaria* consist of funnel-shaped, horn-yellowish capsules arranged in bunch-like groups of 8-33 (in one case a single capsule was found). The capsules are fixed to the hard substrate (rock, stone, shell) by slender peduncles 1.2-1.8 mm long. Their bases are confluent, forming a continuous thin reticular membrane covering the substrate. The capsules are 8-11 mm high; the widened upper end is circular, 5 mm in diameter, slightly concave, surrounded by a narrow rim. In the centre of the upper end is an exit hole, 1.5-1.6 mm in diameter, covered by a semi-transparent membrane. Eggs or embryos can be seen clearly through the membrane covering the exit hole, and also through the smooth translucent walls.

In most of the empty capsules, the exit holes were open. However, in the empty capsules collected in Haifa Bay, the exit holes remained closed, but the walls were torn. Eggs in full capsules were numerous, but could not be counted in preserved material. The capsules collected in Dor (14. VI. 1961) contained embryos with shells (Figure 20b). "The embryo will feed on more eggs and hatch long after the end of metamorphosis." (Bandel, *in litt.* 1977)

Locality	Date	Zone	Depth	Capsules		
				Number in cluster	With eggs	Empty
Haifa Bay	31. VIII. 1974	infralittoral	51 m	11	—	11
Atlit	14. VIII. 1965	intertidal	to 1 m	19	12	7
Dor	16. VIII. 1950	intertidal	to 1 m	1	—	1
Dor	14. VI. 1961	intertidal	to 1 m	9	6	3
Dor	24. VII. 1969	intertidal	to 1 m	8	5	3
Tel-Aviv	15. IX. 1961	intertidal	to 1 m	41	33	8

Distribution of adult animals along the Mediterranean coasts of Israel: Nahariyya, Haifa Bay, Bat-Gallim, Karmel Beach, Shiqmona, Atlit, Caesarea, Mikhmoret, Netanya, Tel-Barukh, Tel-Aviv, Palmahim, Ashqelon.

Vertical Distribution: shallow waters up to 1-3 m depths and in infralittoral zone, 49-71 m depths

Conus ventricosus Gmelin, 1791

(Figure 21)

Record:

BANDEL, 1975: 106-108. Banyuls-sur-Mer

Material:

[det. Klaus Bandel]

Akhziv, 15. VI. 1971 - 1 group of 5 capsules

Caesarea - 2. VII. 1967. 2 groups of 3 and 4 capsules

Mikhmoret - 9. VI. 1964. 3 groups of 3, 5 and 6 capsules

All the egg masses were found in the intertidal zone attached to algae. The egg mass consists of white flattened flask-shaped capsules narrowed at their base, forming a group of 3-6. The capsules are arranged parallel in a row, slightly inclined in one direction. They are attached to the substrate (algae) by a very short peduncle extended into a broad basal membrane; the membranes are confluent into a common base of attachment.

The capsules are 3.6-4.2 mm high. Each capsule is convex on one side and concave on the other. The convex side of the capsule faces the concave side of its neighbour in the row. The walls are thin and tough, the concave side smooth, the convex side with longitudinal ridges (4-6). At the uppermost part of the capsule an elongated slit-like exit hole is covered by a transparent membrane and surrounded by a slightly corrugated collar-like border.

"The size of the capsules varies according to the size of the female. Each capsule contains an average of 11 eggs, which all develop. After a period of 3 weeks' development the cover of the escape aperture is dissolved and crawling juveniles escape. They have accomplished their development within the egg capsule." (BANDEL, 1975)

Distribution of adult animals along the Mediterranean coasts of Israel: Intertidal zone: Akhziv, Akko, Karmel Beach, Shiqmona, Dor, Caesarea, Tel-Barukh, Bat-Yam, Palmahim.

Infralittoral zone: to a depth of 24 m, at Haifa Bay

OPISTHOBRANCHIA

Bulla striata Bruguière, 1789

(Figures 22a, 22b)

Material:

Maagan-Mikhael, 19. IX. 1978 - sea water pond

Eight adult specimens of *Bulla striata* were taken from a sea water pond near the shore at Maagan-Mikhael, S of Haifa, together with a flat yellowish-white ribbon-like egg mass. The animals and the egg mass were placed in an aquarium at Tel-Aviv University.

After 2 days, on 21. IX. 1978, 4 additional egg masses were found attached by the length of one edge of the ribbon to the walls of the aquarium. The ribbons were from 4 to 10 cm long and 0.6 cm wide. The egg capsules embedded in the gelatinous matrix were arranged in transverse double rows (hence the striated appearance of the ribbon). The number of egg capsules in a single row was 100-120; thus, 1 cm length of the ribbon contains about 500 capsules. The capsules are round with smooth walls; their diameter is about 70 μ m. In each capsule is one egg.

Pieces of ribbon were put into dishes for observation. On 25. IX. 1978, 4 days after spawning in the aquarium, rotation of embryos within the capsules was observed. Their body was yellowish with a conspicuous orange spot; the latter disappeared later.

After 8 days, on 29. IX. 1978, the larvae were released from the capsules into the gelatinous coat of the string, whence they made their way into the water. Numerous veligers moved vividly outside the egg ribbon, their almost globular transparent shell of 1½ whorls clearly visible. Many veligers remained alive and active for about 2 weeks. Gradually the ribbons disintegrated; many empty veliger shells were seen remaining in the dish. Numerous ciliates swarmed around the remnants of the egg ribbon.

Similar observations were made on egg masses taken from the same pond on 3. X. 1978.

Distribution of adult animals along the Mediterranean coasts of Israel:

Live: 1) intertidal zone - Akhziv, Mikhmoret

2) infralittoral zone - Haifa Bay, 8-31 m depth

Shells: 1) on the beach throughout the coast

2) infralittoral - Akko, Haifa, Atlit, 15-31 m depth

The abundance of beach shells of *Bulla striata* in contrast to the rare occurrence of living animals was very noticeable.

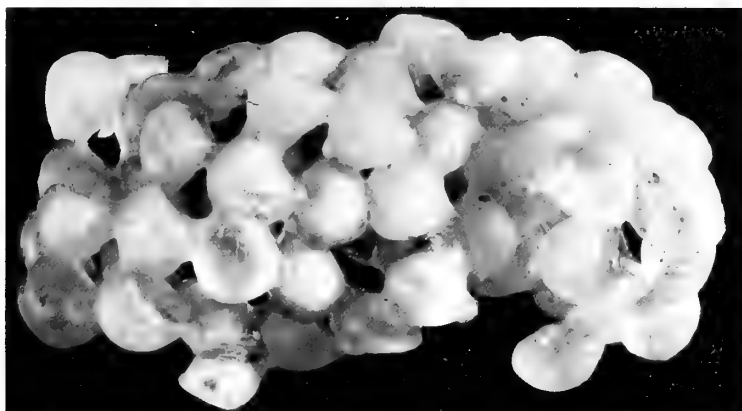


Figure 13 a

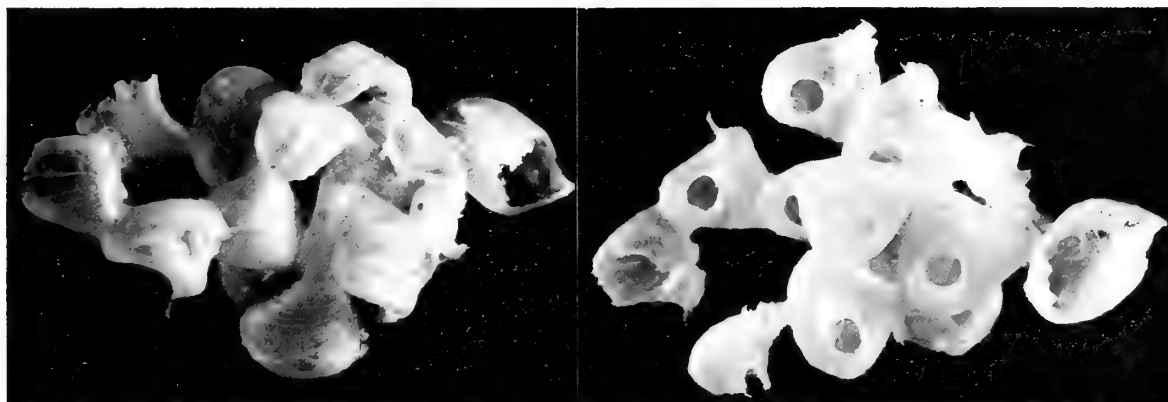


Figure 13 b

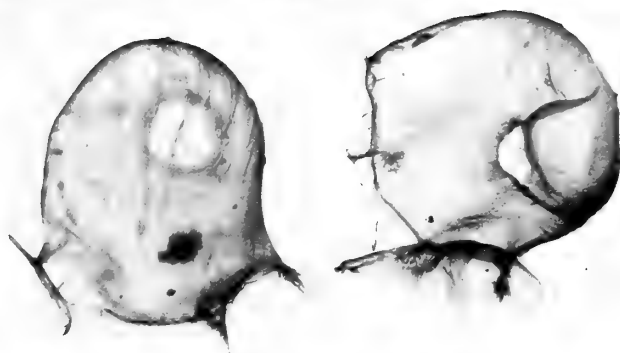


Figure 13 c

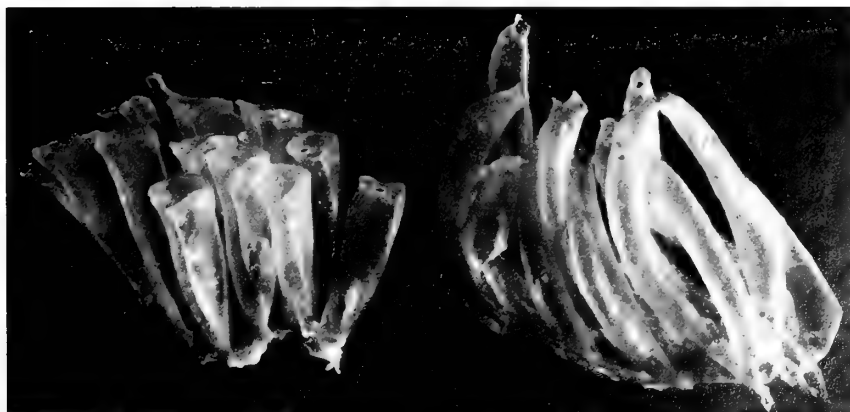


Figure 14



Figure 15

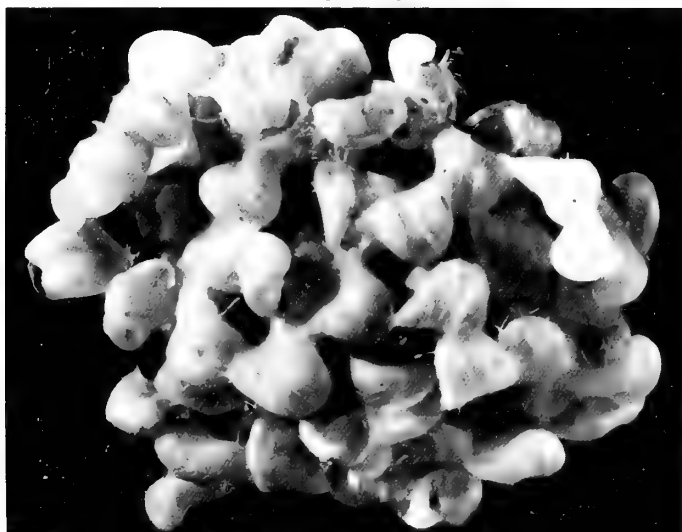


Figure 16



Figure 17

Aplysia fasciata Poiret, 1789

(Figures 23a, 23b)

Record:

BEBBINGTON & THOMPSON, 1968: 4-5. Bassin d'Archon

Material:

[det. Nellie Eales]

Akhziv - 24. IV. 1962; 25. VI. 1962; 8. VII. 1964;
28. VI. 1965; 9. VII. 1974

Netanya - 19. VI. 1969

Tel-Barukh - 23. V. 1970; 3. V. 1975; 4. V. 1977;
7. V. 1977

Tel-Aviv - 20. V. 1971; 31. VII. 1973

Yafo - 6. V. 1962

Palmahim - 20. V. 1976

The egg masses of *Aplysia fasciata* were collected during April-July along the coast among algae (*Ulva*, *Enteromorpha*). The spawn forms long cylindrical, loosely tangled, yarn-like strings; the largest egg mass consisted of about 40 m of strings. Their colour is yellow-brown and the diameter is about 2 mm. Rounded transparent capsules are embedded in the gelatinous matrix; these capsules are arranged 4-6 abreast in transverse rows throughout the entire length of the string. Numerous eggs could be seen through the capsule wall. In 10 capsules examined the numbers of eggs per capsule were as follows: 36, 38, 40, 40, 40, 40, 42, 43, 46, 46, 48 (average ca. 42). Each ovum measured 90-114 μ m. These results agree with those of BEBBINGTON & THOMPSON (1968), who found 118 capsules per centimeter length of the string and 43 ova per capsule; the total number of eggs in the mass 25 877 400.

Ciliary movement of the veliger was observed in the spawn collected on May 3 and 4, 1977. The embryonic shell of the larvae was of 2 whorls with an almost circular aperture (Figure 23b). In some of the larvae the operculum could be seen on the rear part of the foot. After hatching, free swimming veligers were found in the observation dish. "The embryonic period lasts 20-22 days." (Eales, 1971, *in litt.*)

Distribution of adult animals along the Mediterranean coasts of Israel: Akhziv, Akko, Haifa, Dor, Caesarea, Netanya, Arshaf, Tel-Barukh, Tel-Aviv, Yafo, Bat-Yam.

Vertical Distribution: Intertidal zone; infralittoral zone (rarely) 9-24 m deep.

Bursatella leachi savigniana Audouin, 1826

(Figures 24, 25)

Record:

BARASH & DANIN, 1973: 329; fig. 13. Israel

Material:

[det. Nellie Eales]

Dor - 6. VI. 1971, Fishery Research Station, salt water pond

Dor - 21. III. 1971; 15. VI. 1971, Fishery Research Station, aquarium

Maagan Mikhael - 31. I. 1978, salt water pond

Tel-Aviv - 26. III. 1971, Tel-Aviv University aquarium

All egg-laying adult specimens were taken from salt water ponds at Dor and Maagan Mikhael.

The egg masses of *Bursatella leachi savigniana* are laid in gelatinous strings (2-3 mm in diameter), that form a tangled green mass. The limiting membrane of the string and the gelatinous matrix are transparent, and the round membranous capsules embedded in the matrix are clearly visible. The capsules are quite regularly arranged along the string; in 1 centimeter of string there are 160-280 capsules. The eggs within the capsules are greenish.

The eggs in a string deposited on 26. III. 1971 in a Tel-Aviv University aquarium were seen in their early cleavage stages; after 4 days ciliary movement of the veligers was observed. Two to 3 days later, veligers prior to hatching were seen with light brown shells. The string became brittle and free swimming veligers appeared in the observation dish.

Similar observations on *Bursatella leachi guineensis* were reported by BEBBINGTON (1969: 334-338): "There were from 2 to 6 eggs per capsule, 250 capsules per cm. ... Development within the egg string occupies 6 days. ... The embryos later become cloaked with cilia and they begin to rotate in their capsule (at 4 days) ... the larval shell appears (4-5 days)."

Distribution of adult animals along the Mediterranean coasts of Israel: In shallow water, 2-3 m depth: Dor, Mikhmoret, Ashdod; in sea water ponds, near the shore: Dor, Maagan Mikhael; infralittoral zone, 12-37 m depth: off Haifa, Bardawil.

Elysia timida (Risso, 1818)
(Figure 26)

Record:

RAHAT, 1976: 186-193; fig. 2. Jerusalem

Material:

Mikhmoret - depth 0.2-1.0 m on rocks covered with vegetation

"A total of about 90 *Elysia* specimens were collected and from these more than 20 egg masses were obtained. ... Fourteen egg masses were followed through to the hatching of free juvenile larvae. ... In some egg capsules two eggs were found, and occasionally empty egg capsules were observed. After 2-3 days the eggs developed into a veliger form, which moved around in its egg capsule for another 1-2 days. ... Hatching took place after 16-21 days and was completed within 24 hours. Some juveniles left their shells behind, inside the egg mass, while others carried them around for several hours before the shells were discarded." (RAHAT, 1976: 188, 190)

Distribution of adult animals along the Mediterranean coasts of Israel: Akhziv, Akko, Dor, Mikhmoret.

Vertical Distribution: intertidal zone, depth of 0.2-1.0 m

Glossodoris sp.

(Figure 27)

Material:

Mikhmoret - 12. X. 1971, attached to branches of an alga

The small egg mass, 4 mm wide, forms a flat coiled springlike ribbon folded upon itself in 3 volutions. The gelatinous matrix is transparent with minute white capsules of spherical shape densely embedded in it. The capsules are arranged in rows along the band, 3-4 capsules abreast in a row seen from above.

Remarks: *Glossodoris gracilis* is one of 3 species of this genus reported from Israel. The egg mass found seems to be similar to that of *G. gracilis* (HAEFELFINGER, 1963: 706; fig. 1).

Aeolidiella sp.

(Figures 28a, 28b)

Record:

TARDY, 1969: 25 - 29; plt. 14, figs. 5, 6

Material:

7. XI. 1976, 3 egg masses in aquaria, Tel-Aviv University

Three adult specimens of *Aeolidiella* sp. were collected at Bat-Yam on 2. XI. 1976 in the intertidal zone (infra-littoral fringe) on rocks. One specimen was about 40 mm long, the 2 others were ca. 18 mm. They were put into an aquarium for observation. On 7. XI. 1976, 3 ribbon-like pinkish egg masses were found attached to the walls of the aquarium: one egg mass, the longest one, with 2½ coils (width 18 mm), the second ring-like, the third not coiled, nearly straight (20 mm long).

The transparent mucous matrix of the egg mass is limited by a thin membrane. Within the matrix are densely packed many pink-yellowish egg capsules. After 2 days, on 9. XI. 1976, ciliary movements were observed within the capsules, and in many of them veligers with larval shells were clearly seen.

CEPHALOPODA

Sepia officinalis Linnaeus, 1758

(Figures 29a, 29b, 29c)

Record:

MANGOLD-WIRZ, 1963: 101-102. Port Vendres

Material:

Yafa - 15. II. 1962, bunches of 12, 21, 43 eggs and 8 single eggs

Yafa - 3. IV. 1962, 1 bunch of 9 eggs and 5 single eggs

Nizanim - III. 1975, 1 bunch of 52 eggs

Palmahim - 21. IV. 1975, 1 single egg

Bardawil - 2. XI. 1975, 1 single egg

Most egg masses were collected in the intertidal zone during February-April, except one egg taken by dredging in November 1977 at 48 m depth off Bardawil.

The eggs are large, about 8 mm long, 5 mm wide, black-brown, pear-shaped. The colour derives from the ink secreted on the eggs while they are shed. The eggs are attached to the algal branch (*e. g. Cystoseira*) by a flattened ribbon-like stalk. The stalk is twisted around the "stem" of the alga or around stalks of other eggs, thus forming a group resembling a bunch of grapes.

Eight juveniles hatched from the eggs collected at Nizanim in March 1975. They were 10-11 mm long and 4-5 mm wide. The shape of the body was similar to that



Figure 18 a

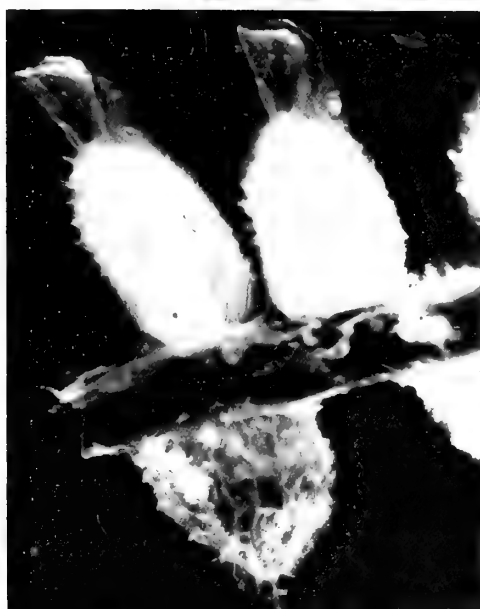


Figure 18 b



Figure 19



Figure 20 a



Figure 20 b

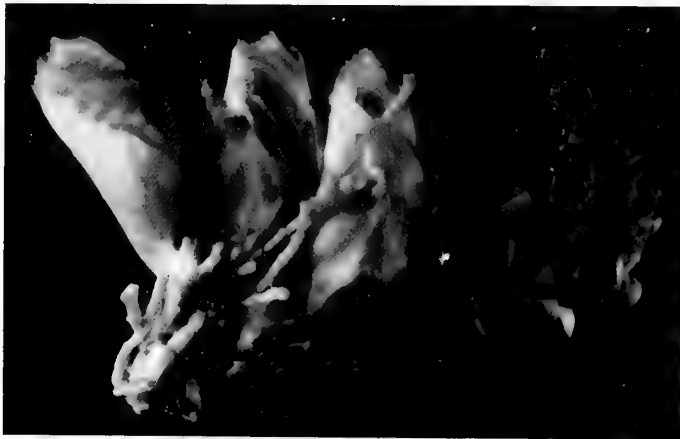


Figure 21

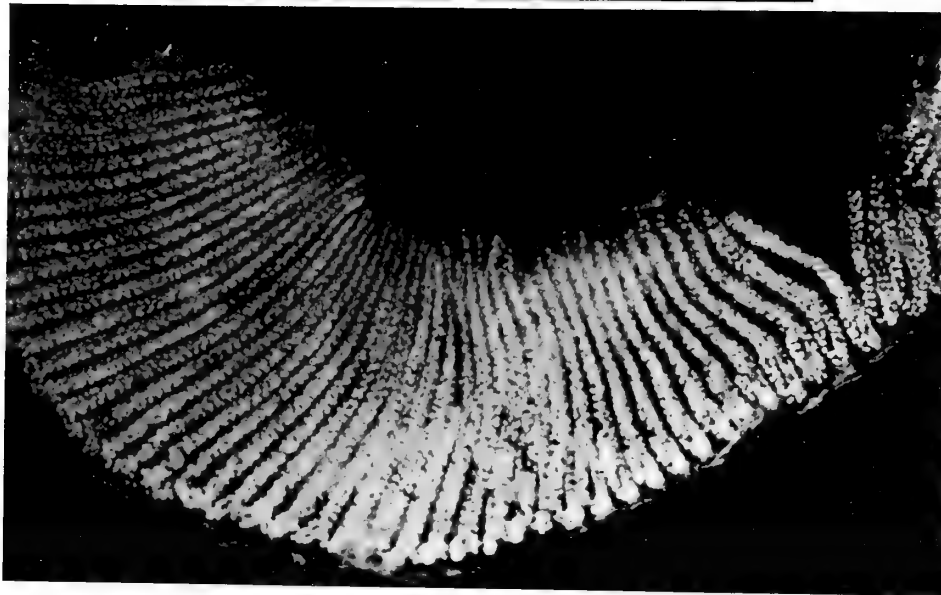


Figure 22 a

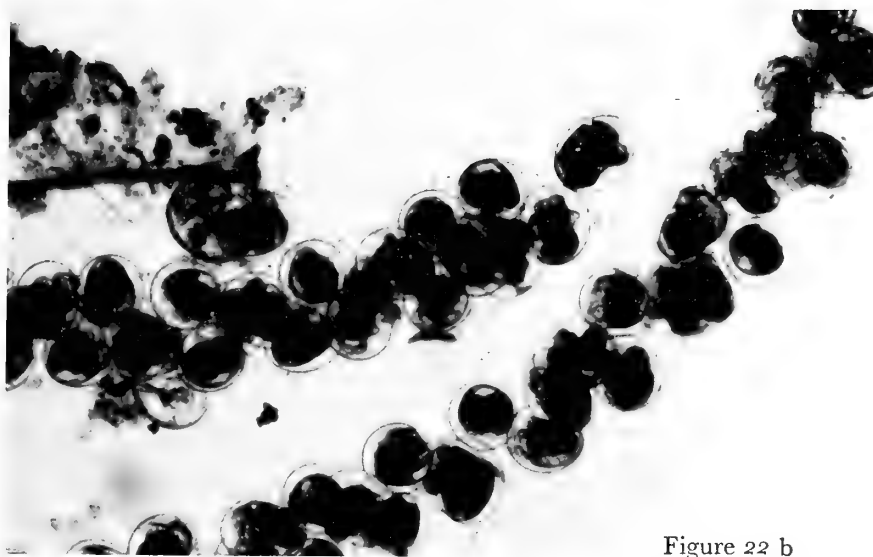


Figure 22 b

of the adult, the head tentacles and eyes distinct. Cuttle bones of the juveniles found in the preserved material had 8-11 growth lines (Figure 32c).

"The egg masses are deposited in littoral waters on sandy or sandy mud bottoms at a depth of 1-30 m. The animals prefer to attach their eggs to solid objects of elongated form. One female lays 200-550 eggs. . . . The young *Sepia* adapts itself immediately to the benthic life of the adults without passing a planktonic phase." (MAN-GOLD-WIRZ, 1963)

Distribution of adult animals along the Mediterranean coasts of Israel: Qishon, Haifa, Caesarea, Atlit, Hadera, Mikhmoret, Alexander River, Netanya, Arshaf, Tel-Barukh, Tel-Aviv, Yafo, Bat-Yam, Rubin River, Ashdod, Ashqelon, Yunis, Gaza, El Arish, Bardawil.

Vertical Distribution: 9-183 m depths, sand, sandy mud, rocks.

Sepia elegans d'Orbigny, 1826

(Figures 30a, 30b)

Records:

BOULIGAND, 1961: 589-594. Banyuls-sur-Mer

MANGOLD-WIRZ, 1963: 116-117. Port Vendres

KNUDSEN, RUBY G. & J. KNUDSEN, 1972: 83-97.

Haifa (3 eggs, 11 juveniles)

Material:

Palmahim - X. 1977, at 65 m, 2 eggs on a tube of a polychaete

The eggs of *Sepia elegans* are deposited and attached singly; they do not form bunches as do those of *S. officinalis*; they are smaller than the latter; they are nearly spherical, 5 mm high, 4 mm wide; they appear yellow because of the ample quantity of yolk within them as seen through the external transparent white-greyish membrane. On the free pole of the egg is found a narrow, unciform projection; similar projections are observed in eggs of many other cephalopod species. A ribbon-like peduncle, white-greyish as the outer membrane arises from the base of the egg and forms a ring around the substrate. The 2 eggs found in Palmahim were attached to a leathery polychaete tube, standing separately one from the other at a distance of a few millimeters. To our knowledge, the finding of an egg mass of *S. elegans* on a tube of *Polychaeta tubicola*, as in our case, has not been reported previously. BOULIGAND (1961) indicates *Octocorallia* (Alcyonacea, Gorgonacea) as substrate for spawn of *S. elegans*.

Distribution of adult animals along the Mediterranean coasts of Israel: Haifa, Dor, Caesarea, Tel-Aviv, Gaza, Bardawil.

Vertical Distribution: in depths of 62-135 m

Table 1

Months of collection or observation of the egg masses

Species	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
<i>Cerithium scabridum</i>										+		+
<i>Cerithium rupestre</i>							+		+			
<i>Rhinoclavis kochi</i>			+									
<i>Janthina nitens</i>												+
Naticidae type A				+								
Naticidae type B			+	+	+							
Naticidae type C				+	+							
Naticidae type D				+	+							
<i>Cassidaria echinophora</i>			+			+						
<i>Semicassis undulata</i>						+		+				
<i>Tonna galea</i>			+					+				
<i>Trunculariopsis trunculus</i>	+				+	+	+	+		+		
<i>Murex brandaris</i>					+	+	+					
<i>Thais haemastoma</i>						+		+				
<i>Thais carinifera</i>								+			+	
<i>Columbella rustica</i>							+	+				
<i>Euthria cornea</i>		+				+	+					
<i>Pisania striata</i>					+	+						
<i>Sphaeronassa mutabilis</i>		+		+	+							
<i>Fasciolaria lignaria</i>						+	+	+	+			
<i>Conus ventricosus</i>						+	+					
<i>Bulla striata</i>									+	+		
<i>Aplysia fasciata</i>				+	+	+	+					
<i>Bursatella leachi savigniana</i>	+		+			+						
<i>Sepia elegans</i>										+		
<i>Sepia officinalis</i>		+	+	+						+	+	

GUIDE TO THE EGG MASSES OF GASTROPODA CONSIDERED IN THIS PAPER

Characteristic features differentiating the egg masses of marine gastropods studied in this paper are reviewed below:

- A. Egg masses laid on solid substrata: rocks, stones, algae, sand, mud
 - a. Eggs within thin-walled, minute capsules (up to 2.5 mm) or within spaces embedded in gelatinous matrix. Egg masses forming strings, ribbons, or sheets
 - I. Egg masses encrusted with particles of sea bottom (sand, mud)
 1. Egg masses forming convoluted strings, eggs in capsules *Rhinoclavis kochi* (Figure 3)
 2. Egg masses forming coiled ribbons - "collars," eggs in spaces Naticidae (Figures 5-8)
 - II. Egg masses not encrusted with particles of sea bottom
 1. Eggs within minute capsules (up to 1.5 mm).
 - * Egg masses cylindrical, long, coiled and tangled.
 - Egg strings yellowish-brown *Aplysia fasciata* (Figure 23a)
 - Egg strings greenish *Bursatella leachi savigniana* (Figure 24)
 - ** Egg masses ribbon-like
 - Ribbons not coiled, flat, yellowish white
..... *Bulla striata* (Figure 22)
 - Ribbons irregularly coiled, greyish
..... *Cerithium scabridum* (Figure 1)
 - Ribbons spirally coiled, white *Elysia timida* (Figure 26)
 2. Eggs within spaces. Egg masses forming sheets of considerable size *Tonna galea* (Figure 11)
 - b. Eggs within capsules with tough pergameneous walls, size moderate to large (2.5-13 mm)
 - I. Egg capsules united to clusters composed of several layers or rows
 1. Clusters tower-like; pillar-shaped capsules arranged in regular layers (tiers)
..... *Semicassis undulata* (Figure 10)
 2. Clusters irregular, capsules interconnected by projections of their walls
 - * No exit hole, capsule cup-shaped, walls without conspicuous ridges *Cassidaria echinophora* (Figure 9)
 - ** Exit hole on a side wall of the capsule; conspicuous ridges on the wall surface

- Capsules tongue-shaped *Murex brandaris* and *Trunculariopsis trunculus* (Figures 12, 13)
- Capsules almost triangular, vase-like, narrowed at their base *Euthria cornea* (Figure 16)
- 3. Clusters bunch-like, exit hole at the top
 - * Capsules pillar-like, broader and flattened at the top *Thais haemastoma* (Figure 14)
 - ** Capsules cylindrical, falciform, narrowed at the top *Thais carinifera* (Figure 14)
 - *** Capsules funnel-shaped, attached to the substrate by a slender peduncle
..... *Fasciolaria lignaria* (Figure 20)
- II. Egg capsules in groups, standing in a row, side by side, attached by a basal membrane to the substrate; exit hole at the upper end
 1. capsules pouch-like; exit hole surrounded by thin projections *Sphaeronassa mutabilis* (Figure 18)
 2. Capsules compressed, flask-shaped; exit hole slit-like *Conus ventricosus* (Figure 21)
- III. Egg capsules laid singly; exit hole at upper end
 1. Capsules oval, attached by their flattened bases to the substrate. Walls transparent with numerous fine ridges *Columbella rustica* (Figure 15)
 2. Capsules cup-shaped, attached to the substrate by a short stalk *Pisania striata* (Figure 17)
- B. Egg masses adhering by mucous strings to the underside of the floating raft produced by the parent, a pelagic snail *Janthina nitens* (Figure 4)

SUMMARY

The present paper intends to provide information on egg masses of molluscs from the south-eastern Mediterranean: Israel and North Sinai. The spawn was collected mainly during the warm season - March through August (see Table 1).

The great majority of egg masses discussed in this work are of gastropods (over 20 species); from other molluscan classes only 2 species of cephalopods are discussed.

The egg masses of gastropods belong to groups in which the eggs are protected by a cover of gelatinous material or by tough capsule walls (see list of species).

The types of hatching stage in the development of the marine gastropods are:

Veligers (pelagic)	<i>Aplysia fasciata</i>
<i>Cerithium scabridum</i>	<i>Bursatella leachi</i>
<i>Rhinoclavis kochi</i>	Veliger (or crawling)
<i>Tonna galea</i>	<i>Thais haemastoma</i>
<i>Thais carinifera</i>	<i>Columbella rustica</i>
<i>Bulla striata</i>	Crawling (or veliconcha)

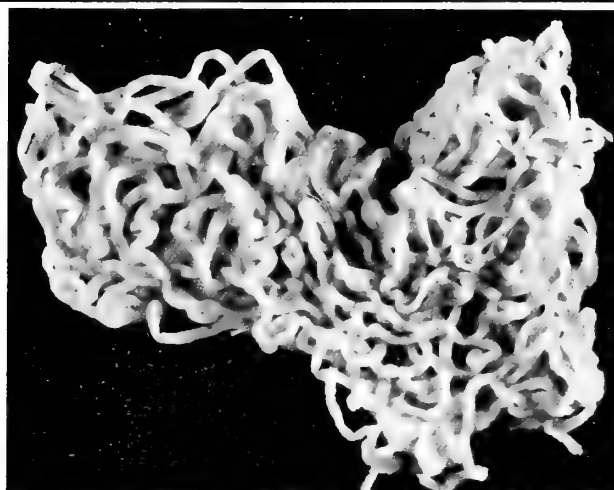


Figure 23a

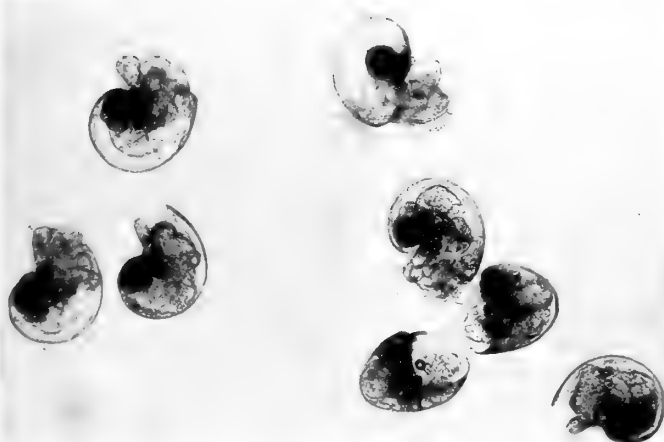


Figure 23b



Figure 24



Figure 25

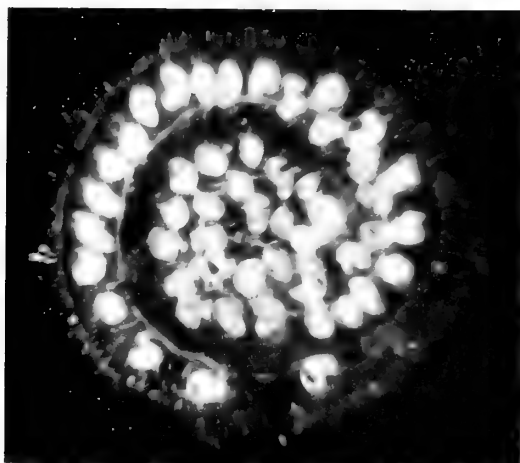


Figure 26

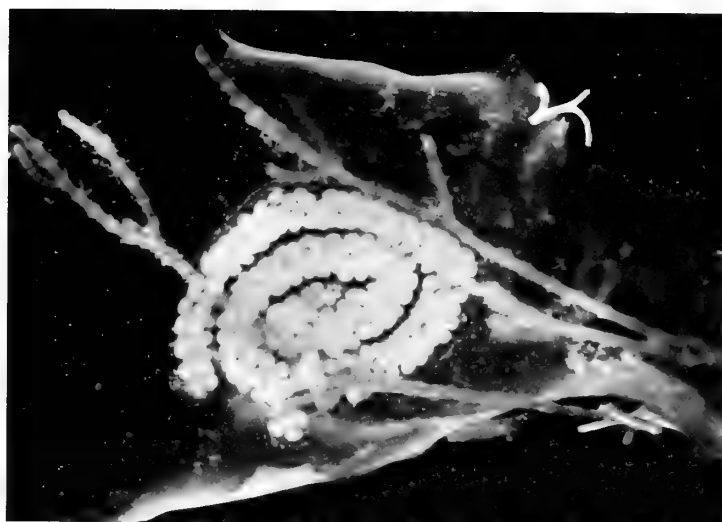


Figure 27

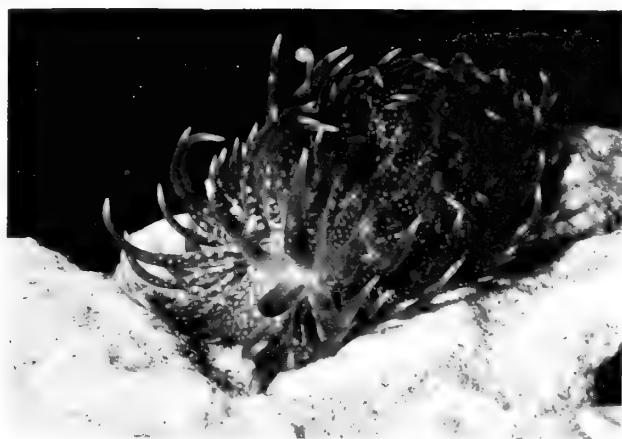


Figure 28 a

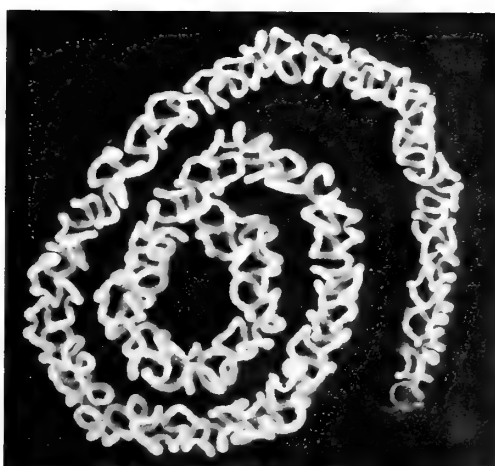


Figure 28 b

Cerithium rupestre *Pisania striata*
Cassidaria echinophora *Sphaeronassa mutabilis*
Trunculariopsis trunculus *Fasciolaria lignaria*
Murex brandaris *Conus ventricosus*
Euthria cornea *Elysia timida*

Among these gastropods are 4 species of Indo-Pacific origin: *Cerithium scabridum*, *Rhinoclavis kochi*, *Thais carinifera* and *Bursatella leachi savigniana*. These species immigrated from the Red Sea through the Suez Canal and at present common along the Mediterranean coasts of Israel. All 4 species mentioned have free swimming

veliger larve. The ability of the larvae to swim and to be carried by currents is obviously of advantage in the process of migration.

From western Mediterranean egg masses or veligers of 195 species of mollusks were recorded.

The number of species of which egg masses are known from the south-eastern Mediterranean (Israel and North Sinai) is thus but a fraction of the species investigated in the western Mediterranean. Spawn of many more species will likely be found in the course of properly organized investigation in the future. (A comparison of the respective numbers is presented in the following table).

	Prosobranchia	Opisthobranchia	Cephalopoda
West Med.	72	81	42
Israel	21 ³	6	2

Data based on the following publications:

Italy (Naples): LO BIANCO, 1909; FRAENKEL, 1927; PALOMBI, 1939;
 BACCI, 1947
 France (Banyuls-sur-Mer, Endoume, Villefranche): FISHER, 1933;

FRANC, 1948; BOULIGAND, 1961; HAEFELFINGER, 1969; BANDEL, 1975; MANGOLD-WIRZ, 1976
 Algiers: FRANC, 1948
 Israel: BARASH & DANIN, 1973; RAHAT, 1976

Notes on the Reproduction of two Freshwater Gastropods *Theodoxus jordani* and *Melanoides tuberculata*

Theodoxus jordani (Sowerby, 1832)
 [= *Neritina jordani* Sowerby, 1832]

(Figures 31a, 31b)

Egg capsules of *Theodoxus jordani* were collected near the shore of Lake Tiberias on 1. XI. 1966 and 19. III. 1973 at a depth of 20-50 cm. The capsules were attached to the shells of *Theodoxus*, living on hard substrata (stones) in the lake and to shells of *Melanopsis*.

The capsules are opaque white, semi-globular, somewhat flattened; their diameter is 1-1.2 mm. The capsular walls are rather thick and rough, composed of organic matrix covered with small sand grains. The capsule consists of 2 halves; the lower half is fastened to the substrate, the suture between the two halves is almost at the equator. Most capsules were "open" and empty, the upper lid broken off, probably when the young escaped.

"... small sand grains or diatom cases derived from the faeces stored in the rectum in a "Crystal sac" and poured over the capsule as it is laid. ... The capsules contain about 70 eggs each 110-125 μ m in diameter and uncoloured. Only one egg develops, the rest being used as food and the young snail hatches in crawling stage with a shell about 0.8 mm in diameter." (FRETTER & GRAHAM, 1978: 105, on *Theodoxus fluviatilis*)

Distribution of adult animals of *Theodoxus jordani* in Israel: Freshwater bodies - Lakes (Hula, Tiberias); Rivers (Jordan); Canals (Bet-Shean); brooks, springs, etc.

Melanoides tuberculata (Müller, 1774)

(Figures 32a, 32b)

Melanoides tuberculata is one of the most common gastropod species in the freshwater bodies of Israel, living on muddy and fine sandy bottoms. The first record on the reproduction of *Melanoides tuberculata* in Israel (from

Lake Tiberias, Sea of Galilee) was published by TCHERNOV (1975: 173). The snails treated in the present paper were observed in a freshwater aquarium of Tel-Aviv University; they were originally taken from ponds in Neot-Hakikar (Dead Sea area). Hundreds of specimens have been living in aquaria for 2-3 years and reproducing there throughout the year. Embryos in the brood pouch were easily detected after crushing the shell of the snail. Shelled embryos were found particularly inside the body whorl; their size ranged from 1.5 to 2.2 mm.

The ovoviviparity of *Melanoides tuberculata* is well known (BINDER, 1959; MORRISON, 1954) and of particular interest is the phenomenon of parthenogenesis in this species (JACOBS, 1957). The embryos developing in the mantle cavity leave the "mother" resembling the adult snails.

Specimens were taken at random from the population of the aquarium; they were of various sizes, the largest being 18 mm high. Almost every specimen of minimum height of 10 mm contained embryos. The height of the adult animals and the number of shelled embryos examined in 20 shells were as follows:

Adult height in mm	6	8	9	10	10	10	11	11.5	11.5	12
Number of embryos	0	0	0	0	2	3	2	3	4	4
Adults height in mm	12	12.5	13	13	14	14	15	15	17	18
Number of embryos	5	4	4	4	6	0	5	8	6	13

"As a consequence of their parthenogenicity one individual suffices to found a new colony." (STARMÜHLNER, 1974: 161)

Distribution of adult animals of *Melanoides tuberculata* in Israel: Hula, Lake Tiberias, Jordan River; freshwater bodies in Dead Sea area (slightly saline); rivers in the Mediterranean coastal plains.

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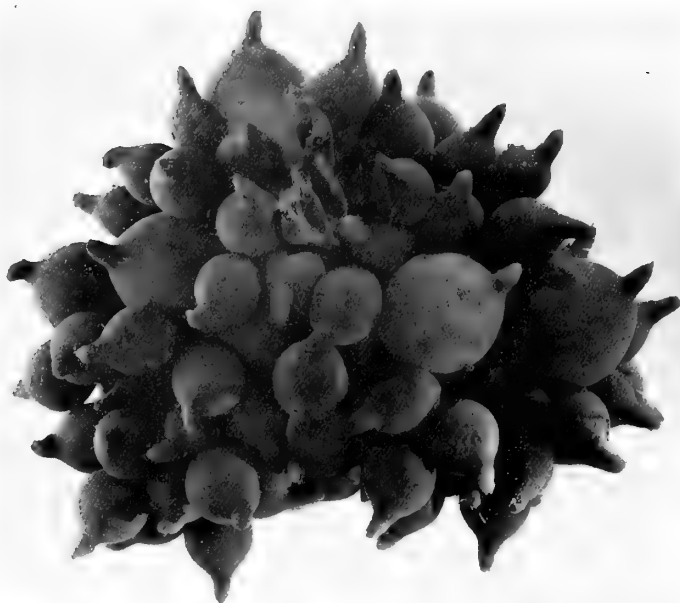


Figure 29 a



Figure 29 b

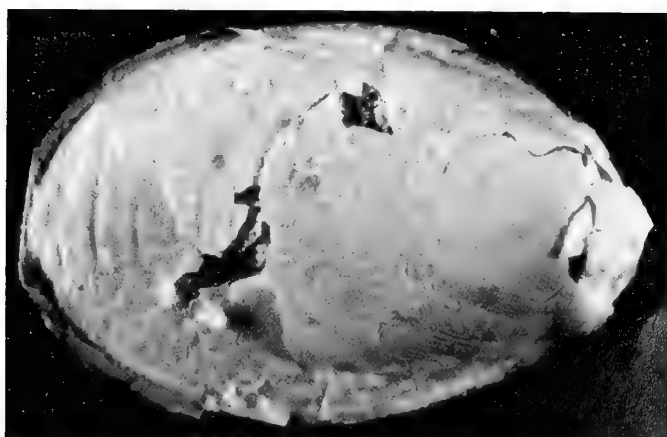


Figure 29 c

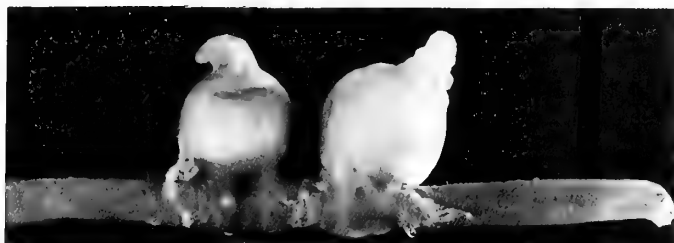


Figure 30a



Figure 30b



Figure 31b

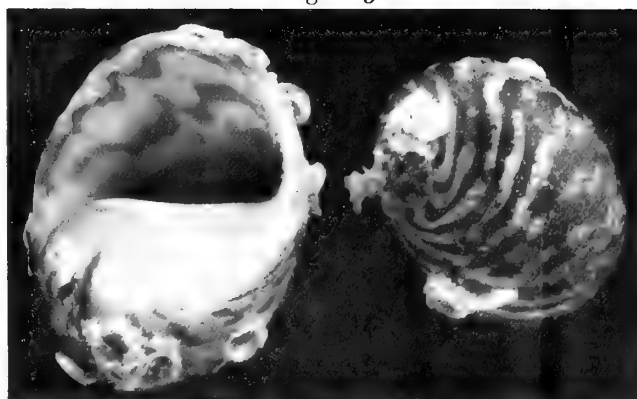


Figure 31a



Figure 32a

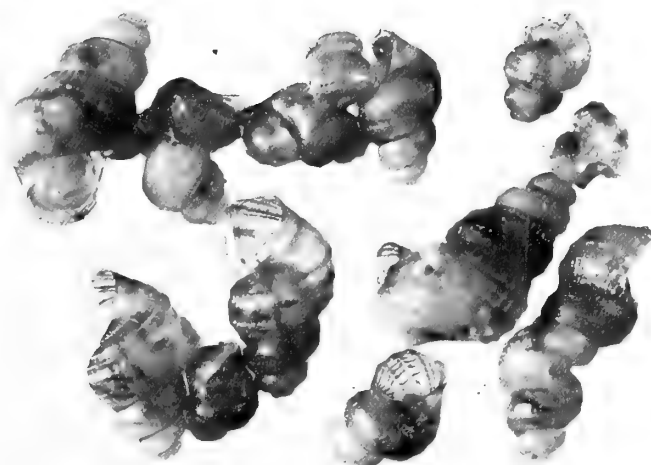


Figure 32b

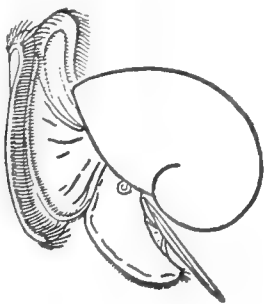
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- Figure 18a: *Sphaeronassa mutabilis* (Linnaeus, 1758), egg mass
Figure 18b: *Sphaeronassa mutabilis* (Linnaeus, 1758), a single
capsules
Figure 19: Nassariid species, egg mass
Figure 20a: *Fasciolaria lignaria* (Linnaeus, 1758), a group of
capsules
Figure 20b: *Fasciolaria lignaria* (Linnaeus, 1758), embryos before
hatching (taken from a capsule)
Figure 21: *Conus ventricosus* Gmelin, 1791, egg mass
Figure 22a: *Bulla striata* Bruguière, 1789, egg ribbon
Figure 22b: *Bulla striata* Bruguière, 1789, capsules with veligers
Figure 23a: *Aplysia fasciata* Poirer, 1789, spawn
Figure 23b: *Aplysia fasciata* Poirer, 1789, veligers
Figure 24: *Bursatella leachi savigniana* Audouin, 1826, adult and
spawn
Figure 25: *Bursatella leachi savigniana* Audouin, 1826, parts of
egg string
Figure 26: *Elysia timida* (Risso, 1818), egg mass (after M. Rahat)
Figure 27: ? *Glossodoris* sp., egg mass
Figure 28a: ? *Aeolidiella* sp., adult
Figure 28b: ? *Aeolidiella* sp., egg mass
Figure 29a: *Sepia officinalis* Linnaeus, 1758, eggs
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Figure 30a: *Sepia elegans* d'Orbigny, 1826
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Figure 31a: *Theodoxus jordani* (Sowerby), egg capsules attached
to shells of adults
Figure 31b: Capsules of *Theodoxus jordani* (Sowerby) on *Melan-
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Figure 32a: *Melanoides tuberculata* (Müller), adult female
Figure 32b: *Melanoides tuberculata* (Müller), juveniles taken from
female's brood pouch

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Aligena laterodentata,
New Species, from the Caribbean Coast of Honduras
(Bivalvia : Leptonacea)

BY

HAROLD W. HARRY¹, JOSEPH C. BRITTON², AND RODNEY NUNLEY²

(5 Text figures)

THE ACCOUNT OF THE LEPTONACEA (CHAVAN, 1969) in the Treatise on Invertebrate Paleontology (MOORE, Ed., 1969) was in press when the review of the genus *Aligena* was published by HARRY (1 January 1969). Chavan's concept of *Aligena*, both with regard to the shell dentition and family relationships, differs from the concepts of generic and family limits as construed by OLSSON (1961), HARRY (1969), KEEN (1971) and others. KEEN (1971) re-allocated a species from the Pacific coast of Middle America, *Aligena obliqua* Harry 1969, to the genus *Orobitella* Dall, 1900. She noted that a second species, *Aligena cerritensis* Arnold, 1903, - at least the Recent members of this species as interpreted by Harry, - is probably a junior synonym of *Orobitella trigonalis* (Carpenter, 1857).

An additional species of *Aligena*, recently found on the Caribbean coast of Honduras, contributes significantly to elucidating the limits and relationships of supraspecific taxa in the Leptonacea.

Aligena laterodentata Harry, Britton and Nunley,

spec. nov.

(Figures 1-5)

Shell white, thin, translucent, inflated, large for the genus: the holotype, a left valve, is 8.5 mm long, 7.2 mm high and 3.1 mm semi-diameter. It is sub-reniform in profile. The prominently inflated umbos touch each other, are prosogyrous, and located midway the length of the shell. A persistent protoconch is 0.21 mm long. Anterior and posterior margins of the adult shell are evenly rounded, of equal

curvature and length; the ventral margin is deeply and broadly sinuate in the middle. A prominent, wide sulcus, vaguely defined, extends nearly to the umbo and ends at the marginal sinus. There is no lunule, escutcheon or corselet. The ligament is not visible externally. The outer surface is swollen, somewhat more so before than behind the sulcus. The surface is evenly sculptured with prominent growth striae, closely spaced and regular.

The interior is very smooth, non-nacreous. The shell margin is thin and without sculpture. The sub-umbonal cavity is very deep. The two adductor muscle scars are about equal in size, sub-rectangular, and joined with a pallial line without a sinus (the line not evident in the holotype).

The hinge plate is divided into anterior and posterior parts, completely separated below and slightly behind the

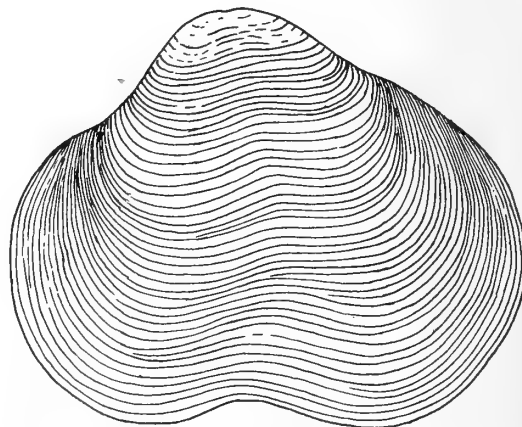


Figure 1

Aligena laterodentata Harry, Britton & Nunley, spec. nov.
External view of left valve of the holotype, 8.5 mm long

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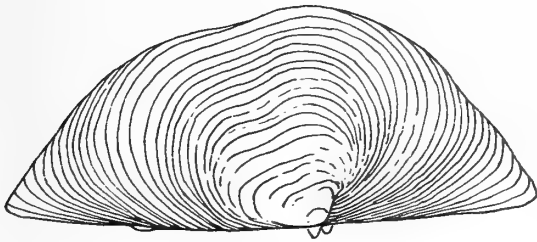


Figure 2

Aligena laterodentata Harry, Britton & Nunley, spec. nov.
Dorsal view of the same shell as in Figure 1

umbo. The posterior part contains the resilium in an elongate resilifer groove, which slopes downward and backward from the anterior end of this part of the plate. The posterior plate is widest just behind the resilifer, where it projects ventrally as an obtuse point. Behind this point there is a single, elongate, posterior lateral tooth in the left valve with a deep groove margining it above, for the reception of the upper of two posterior lateral teeth in the right valve. The latter teeth are separated from each other by a very deep groove forming a socket for the left lateral tooth. The upper lateral of the right valve is much smaller than the lower one. No anterior lateral teeth are present in either valve.

There are two cardinal teeth in the left valve, the larger at the hind end of the front hinge plate, the smaller sep-

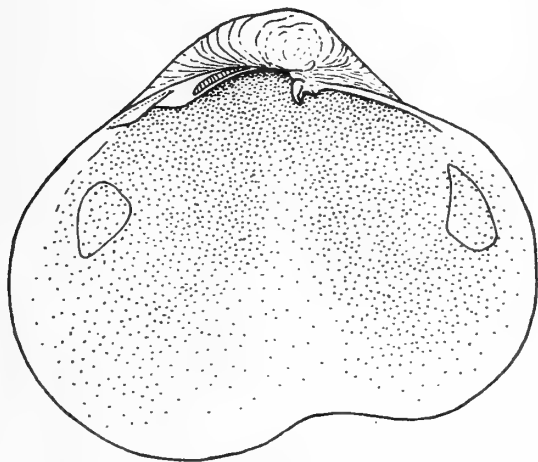


Figure 3

Aligena laterodentata Harry, Britton & Nunley, spec. nov.
Internal view of the same shell as in Figure 1

arated from it by a nick in the plate. Both cardinals are finger-shaped, projecting across the midline. The right valve has only a single cardinal tooth, similar in size and shape to the larger one of the left valve. On the dorsal margin of the left valve a deep, narrow groove extends forward from the gap between the two parts of the hinge plate to the umbo. No comparable gap is present in the right valve, but a large boss, elongate antero-posteriorly, sub-cylindrical, with rounded ends, seems to be attached to the hind end of the front part of the hinge plate and to extend backward, covering the gap between the two parts of the plate. This does not seem to be a tooth in the strict sense.

Seven right and 7 left unmatched valves have been examined. They are only slightly worn, but lack periostracum. The holotype is a left valve, number 781442 of the molluscan collection of the U.S. National Museum of Natural History. Three paratypes are number 781443 of that museum. Other paratypes are in the molluscan collection at Texas Christian University.

The type locality is Calabash Bight (Manatee Bight), along the southern shore of Roatan Island, off the Caribbean coast of Honduras. Specimens were collected in fine-grained sediments associated with *Thalassia* beds at a water depth of approximately 3 m. The species is relatively common as shell material in the type locality, occurring in densities calculated to be 20 to 30 specimens per square meter. No living specimens have been recovered. NUNLEY (1979) presents a comprehensive review of the type locality and its molluscan fauna.

In size, shape and sculpture *Aligena laterodentata* is similar to *A. cokeri* Dall, 1909, from the west coast of Middle America, and to *A. salamensis* (Jaekel and Thiele, 1931) from the Indopacific faunal realm. The similarity is so great that removing it to another genus or subgenus because it has an extra cardinal tooth and posterior lateral teeth would at present be unwarranted. No other species of *Aligena* is known to have lateral hinge teeth, or more than a single cardinal tooth in each valve, CHAVAN's (1969) interpretation of the genus notwithstanding (see below).

OLSSON (1961) and KEEN (1962, 1971) admit that *Orobitella* Dall, 1900, is very similar to *Aligena*, and they include both genera in the Montacutidae. The characters which separate the two genera are relative differences, that is, differences in degree of continuous variables. The most prominent character whereby the two genera have been separated is the position of the umbos. They are midway the length of the shell or only slightly behind that point in *Aligena*, which is thus equilateral or nearly so. The umbos are distinctly behind the midpoint of the shell

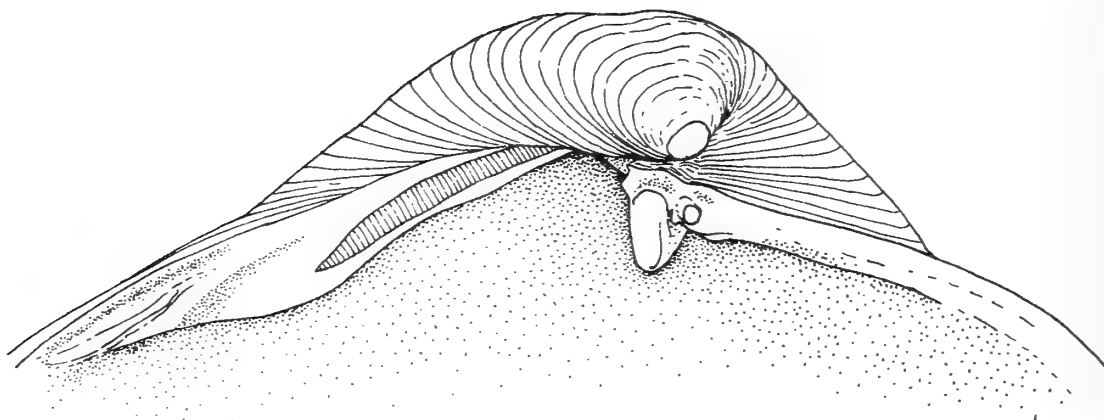


Figure 4

Aligena laterodentata Harry, Britton & Nunley, spec. nov.
Enlargement of the hinge of the same shell as in Figure 1

length in *Oorbitella*, so that the anterior end of the shell is somewhat longer than the posterior end.

If the two species included by HARRY (1969) in *Aligena* are transferred to *Oorbitella*, as KEEN (1971) has done, the limits of form of the species relegated to each genus achieve more precision. Very distinctive of most species remaining in *Aligena* is the median sulcus on the surface of the shell, resulting in a sinuate ventral margin and

transforming an essentially quadrate profile into one that is slightly or distinctly reniform. In the type species, the Miocene *A. aequata* (Conrad, 1834), as well as in the Recent species from the coast of New England, *A. elevata* (Stimpson, 1851), the sulcus is absent. It was not found in the holotype of *A. nucea* Dall, 1913, of the Gulf of California, but it occurs in other specimens of that species as interpreted by HARRY (1969). The sulcus is present in

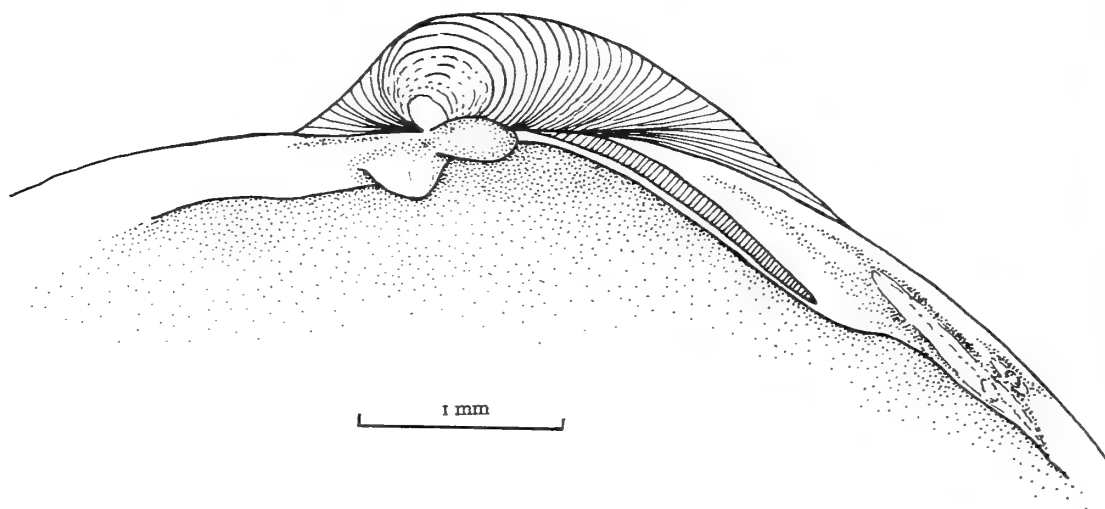


Figure 5

Aligena laterodentata Harry, Britton & Nunley, spec. nov.
Right valve, enlargement of the hinge

A. texasiana Harry, 1969, *A. cokeri* Dall, 1909, *A. salamensis* (Jaekel and Thiele, 1931), and it is very prominent in *A. laterodentata* spec. nov.

ROSEWATER (1968) has proposed that behavioral differences may be correlated with the prominence of the sulcus among species of *Aligena*. He noted that on the Pacific coast of Panama, *A. cokeri* lives firmly attached to the exterior of the tube of the polychaete, *Mesochaetopterus alipes* Monroe, 1933. On each side of the attachment there is a hole through the tube, apparently serving as incurrent and excurrent passages, respectively, for water circulating through the mantle cavity of the bivalve. He further suggested that this unusual arrangement may be correlated with the prominent sulcus of the shell, which coincides with the position of the byssus. In support of this interpretation he noted that *Aligena elevata*, the life habits of which were extensively described by GAGE (1968, as *Montacuta elevata*), has only a flimsy and temporary byssal attachment to the exterior of the tube of the polychaete with which it lives, *Clymenella torquata* (Leidy, 1855), and *A. elevata* lacks the furrow and sinus on the exterior of the shell.

The peculiar rounded appendage on the hinge of the right valve of *A. laterodentata*, in the space between the two parts of the hinge plate, may represent a calcified part of the ligament. Only a fragment of this structure was present in the other specimens examined. This may be the same structure which KEEN (1962) found in *Orobitella* (*Isorobitella*) *singularis* Keen, 1962, from San Quentin Bay, west coast of Baja California. The hinge appendage of *A. laterodentata* fits her description of it in *O. singularis* very well, but the figure she presented is of little help (*op. cit.*, p. 324; fig. 4c, reproduced by CHAVAN, 1969, p. N532, fig. E34, 2b).

Incidentally, *O. singularis* Keen, 1962, was not included in her monumental work on the Sea Shells of Tropical West America (KEEN, 1971) because it was found north of the limit of the area covered. She did mention it briefly in conjunction with another species (*op. cit.*, p. 144). However, *O. singularis* seems to be identical with "*Orobitella* sp." from Sechura, Peru, figure 4 of Plate 35 of OLSSON (1961), which is not dealt with in the text of that work, nor apparently noticed elsewhere.

CHAVAN'S (1969:N523 of volume 2) cryptic account of the hinge dentition of the genus *Aligena* is as follows: "Hinge with small 3a, stout 1, curved 2a in prolongation of an anterior lateral, with small 2b behind it; wide oblique ligament and single strong posterior lateral on each valve." By decoding this cryptogram according to the apparent key, found on pages N53-N56 of the first volume of this

part of the Treatise (MOORE, 1969, Editor), the following translation results: Hinge with (a) small (cardinal tooth and a) stout (one before it in the right valve, a) curved (cardinal tooth) in prolongation of an anterior lateral (tooth), with (a) small (cardinal tooth) behind it (in the left valve); etc.

This is inconsistent with the description of the Kelliidae (CHAVAN, 1969: N522) in which family Chavan placed *Aligena*, for of the family he says there are "no distinctly elongate anterior laterals . . ." The figure of "*Aligena aequata* (Conrad)", numbers 7a and 7b of figure E27 on page N524, have the hinge structure poorly shown, but they seem to indicate a single, long, posterior lateral tooth in each valve, plus two cardinal teeth in the left valve, the larger of which is a continuation of a long anterior lateral lamella; whether cardinal teeth or an anterior lateral tooth are present in the right valve (his fig. E27, No. 7a) is a matter of interpretation of a very ambiguous drawing. His figures are apparently originals, not previously published, but the source of the specimens is not stated. They depict a much more quadrate shell, with straight, truncated anterior and posterior margins and more inflated umbos, than the topotypic *Aligena aequata* (Conrad, 1834) which HARRY (1969: 165-166, figs. 1-3) studied at the U.S. National Museum of Natural History. Chavan's species is evidently not the same one.

ACKNOWLEDGMENTS

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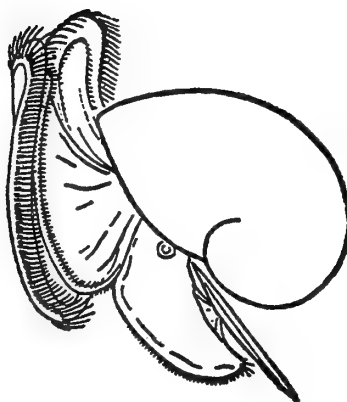
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The Lamellariidae of the North Eastern Pacific

BY

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(2 Plates; 15 Text figures)

INTRODUCTION

THE FAMILY LAMELLARIIDAE (Orbigny, 1841) has been in taxonomic disarray since the description of its first species. Characterized around *Lamellaria perspicua* (= *Helix perspicua* Linnaeus, 1758) and *Lamellaria latens* (= *Bulla latens* Müller, 1776), modern taxonomists are even in disagreement concerning the status of the type species. The specific designation *Lamellaria* proposed by Montagu (1815) has even drawn protest (BERGH, 1886b) because of its resemblance to that of an algal genus, *Laminaria*.

It is not the intention of this paper, however, to review the higher taxonomic nomenclatural problems of the family, but rather to address the specific designations of the species occurring in the North Eastern Pacific. The specific designation *Lamellaria* Montagu, 1815, is used in good faith over *Marsenia* (Leach) Oken 1823, due to its recent and seemingly wide acceptance (including: THIELE, 1931; WENZ, 1938; BURCH, 1946; LAROCQUE, 1953; FRETTER & GRAHAM, 1962; MARCUS & MARCUS, 1967; McLEAN, 1969; KEEN, 1971; THOMPSON, 1973, 1976; YONGE & THOMPSON, 1976).

The North Eastern Pacific lamellariids are abundant, although comprising only a few species. Often overlooked, they include some of the most fascinating deceivers in the phylum Mollusca.

While trying to identify several species, it became apparent to me that the existing nomenclature of the family is confusing and sometimes contradictory. Due to a paucity of information concerning body form, coloration, radulae, and due to the unavoidable reliance on shell descriptions, many of which are not diagnostic, this family has been overlooked by most molluscan guides or handled in a perfunctory manner in the few references that acknowledge it.

Historically, the family has been studied with opisthobranchs due to their shell-less appearance and resemblance to certain dorid nudibranchs (BERGH, 1908; MARCUS &

MARCUS, 1958, 1959, 1960, 1969). Of ecological interest and receiving some attention, is their close resemblance to compound ascidian tunicates upon which they feed and live (HERDMAN, 1893; ANKEL, 1935; GHISELIN, 1964; THOMPSON, 1973), and their ability to secrete acid from the mantle to fend off predators (THOMPSON, 1960, 1969, 1976; YONGE & THOMPSON, 1976).

A review of the diagnostic features of the group has proven some features to be more useful and reliable than others and also presented a question as to the validity and placement of several species. This paper presents a synthesis of the North Eastern Pacific lamellariids with comments concerning their identification, an artificial key and notes on their natural history. Presented also is a taxonomic reallocation.

MATERIALS

Materials from the following museums were examined: California Academy of Sciences, San Francisco, California (CASIZ); Los Angeles County Museum of Natural History, Los Angeles, California (LACM); Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH); as well as the private collections of Donald B. Cadien (DBC), R. Henderson (RH), Gary McDonald (GM) and Carol Skoglund (CS). Due to the preserved state of most of the above material, little information could be gleaned concerning the form and color of the living animals. Fortunately, live specimens of all species except *Lamellaria perspicua* and *L. inflata* were available for examination. Animals were studied in their original habitat, using SCUBA as well as in laboratory aquaria. Color transparencies and preserved voucher specimens have been deposited for future reference at CAS, LACM and SBNHM. Localities referred to in the text are shown in Figure 1.

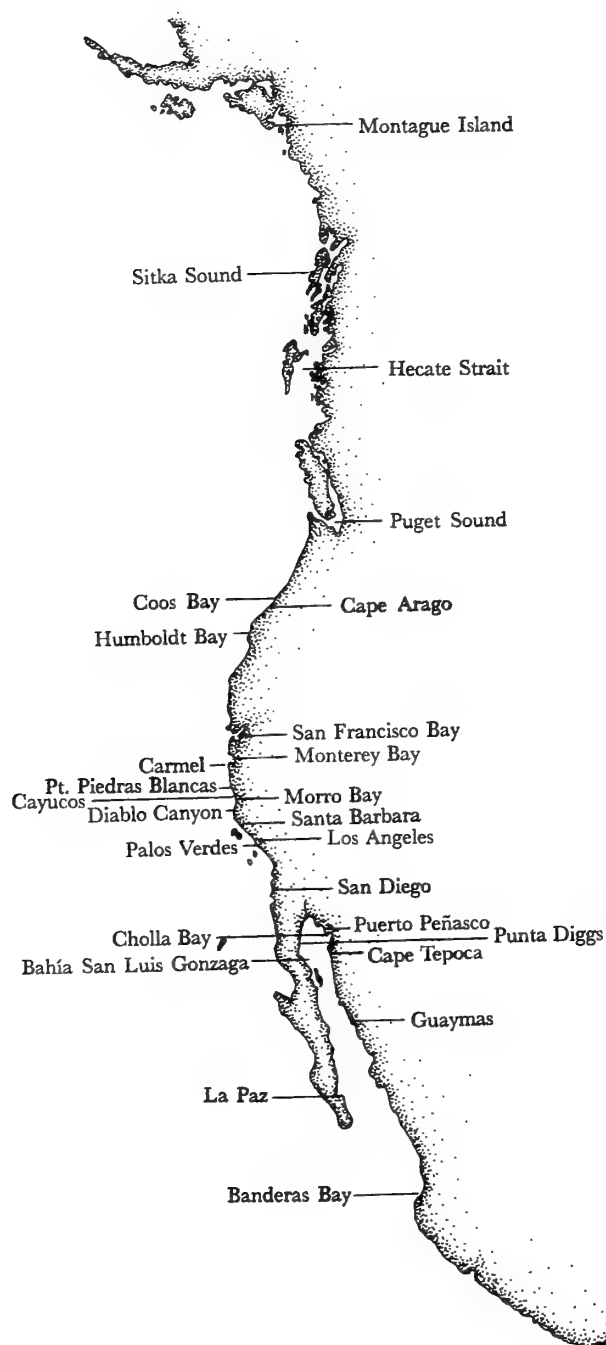


Figure 1

Map of the North Eastern Pacific

NOMENCLATURAL PROBLEMS

Of the original 7 species included in the family Lamellariidae on the Pacific Coast, 4, *Lamellaria stearnsii*, *L. rhombica*, *L. orbiculata* and *L. inflata*, were described by their various authors solely on the basis of shell morphology, with no description of mantle or radulae. For only one species, *Lamellaria perspicua*, was the radula described (MARCUS & MARCUS, 1967).

DALL (1871) described two species and a subspecies from the same locality. The major differences between the three taxa were the presence of a dorsal pore in the mantle of one and size differences between the remaining two. Supplemented by notes from R. E. C. Stearns, the collector, the description of *Lamellaria stearnsii* was based upon two beach-washed shells; *L. stearnsii* var. *orbiculata* on 5 specimens; and *L. rhombica* on two specimens. Purely qualitative, Dall's description gives little diagnostic information to separate the 3 species, and at one point he states, ". . . I should have hesitated about describing them as more than varieties, if it were not that differences appear in the soft parts also" (DALL, 1871: 123). These differences were not observed by Dall, but communicated to him by Stearns who had the benefit of fresh material. In a later paper, DALL in ORCUTT (1885) suggests that *Lamellaria stearnsii* and its variety *L. s. orbiculata* might only be sexually distinct, and he retains *L. rhombica* as a valid species. Due to the overlapping ranges of the two subspecies, I follow DALL in ORCUTT (*op. cit.*), BURCH (1946), SMITH & GORDON (1948) and TALMADGE (1966) in synonymizing them. DALL in ORCUTT (*op. cit.*) states that *L. rhombica* "proves" to be a *Marsenina* Gray (1850) and should take the name *Marsenina rhombica*. He gives no data or reason, however, for this placement.

Examination of the type specimens of all 3 species by Dr. James H. McLean, LACM, revealed the shells to be indistinguishable (personal communication, James H. McLean). During my investigation, I collected hundreds of animals whose shells could fit both descriptions. At variance with Dall's description, each of these specimens had a pore in the mantle revealing the shell. This point was reported previously by GHISELIN (1964). I believe Dall's original intention for separating *Lamellaria stearnsii* and *L. rhombica* was based upon the presence of a pore in the mantle; however, in the absence of an animal lacking a pore, his *L. stearnsii* will require a redefinition. Concerning the heritage of the names of the two similar California species and their proper generic placement, descriptions and proposed placement follow.

To confuse the nomenclature further, *Lamellaria perspicua*, *L. stearnsii* and *L. diegoensis* were assigned to the genus *Marsenia* (Leach) Oken 1823, a junior synonym of *Lamellaria* (Montagu), by BERGH (1886b).

BERGH (1886b), MACGINITIE & MACGINITIE (1949), MARCUS & MARCUS (1967) and KEEN (1971) carry *Lamellaria orbiculata* raised to species level, although DALL in ORCUTT (1885) dubbed it *nomina dubia*. I believe the report of *L. stearnsii orbiculata* from the tropical waters of the Gulf of California (MACGINITIE & MACGINITIE, 1949; KEEN, 1971) to be in error as *L. stearnsii* is a temperate species. The species they refer to as a "white lamellariid" is most probably *L. diegoensis* which is commonly collected on white tunicates in the northern Gulf. An unexplained version of the spelling of *Lamellaria stearnsii* appears in YATES (1890) and later in HOWARD (1972) where it appears as *Lamellaria stearnsiana*.

A more recent report even multiplies problems within the family. ABBOTT (1974) suggests that *Marseniopsis sharonae* is a dwarf or juvenile of *Lamellaria rhombica*. This suggestion is presented without supporting evidence and, I believe, is unfounded.

LAMELLARIIDAE

The shell is internal, concealed or fully enveloped in the mantle, which is not retractile. Naticoid in form, the shell is few whorled, with a periostracum. The aperture is large, the suture impressed. An operculum is lacking. Mantle shape, texture and color are highly variable. Members of the family have shown remarkable concealing ability, the mantle resembling closely the compound ascidian species upon which they prey. Species are represented by both monoecious and dioecious forms.

The Lamellariidae are also characterized by the larval shell, a type referred to as echinospira (FRETTER & GRAHAM, 1962). The echinospira shell is double, one shell within the other. This adaptation is reported to aid the buoyancy of the swimming veliger (McCLOSKEY, 1973).

GASTROPODA

MESOGASTROPODA

LAMELLARIIDAE

Lamellariinae

Lamellaria Montagu, 1815

Marsenina Gray, 1850

Marseniopsis Bergh, 1886

GENERIC SEPARATION

Three factors have proven valuable in separating the Eastern Pacific genera of the family: 1) radula, 2) reproductive type and 3) presence of a dorsal fissure or pore in the mantle: see Figure 2 (modified from BERGH, 1886 a&b).

Radula	Reproductive Type	Dorsal Pore	Genus
0 · 1 · 1 · 1 · 0	Dioecious	Absent	<i>Lamellaria</i>
2 · 1 · 1 · 1 · 2	Monoecious	Present	<i>Marseniopsis</i> <i>Marsenina</i>

Figure 2

Separation of Genera

SPECIES DESCRIPTION

For the purpose of clarity, the following descriptions are limited strictly to the diagnostic characteristics unique to the individual species, such as mantle shape, texture and color, radula, etc. Shell descriptions, although unreliable for species identification, have been included.

Lamellaria Montagu, 1815

The genus *Lamellaria* in the Eastern Pacific can be characterized by separate sexes, the absence of marginal teeth on the radula and a shell entirely enveloped in a non-retractile mantle.

Type Species: *Lamellaria tentaculata* Montagu, 1815 (= *Bulla latens*) (fide WINCKWORTH, 1932; BURCH, 1946)

References and Synonymy:

Lamellaria perspicua (Linnaeus, 1758)

(Figures 3, 4)

Helix perspicua Linnaeus, 1758.*Lamellaria perspicua* (Linnaeus, 1758). THIELE, 1931: 266.

KEEN, 1971: 483. ABBOTT, 1974: 145.

Marsenia perspicua (Linnaeus, 1758). BERGH, 1886b: 13.*Lamellaria perspicua perspicua* (Linnaeus, 1758). MARCUS & MARCUS, 1967: 145.*Lamellaria perspicua mopsicolor* DUBOIS-REYMOND MARCUS, 1958. MARCUS, 1959: 14; 1963: 51. GHISELIN, 1964: 123. MARCUS & MARCUS, 1967: 148. KEEN, 1971: 483. ABBOTT, 1974: 145.

Material Examined:

- 1 specimen, intertidal, Puerto Peñasco, Mexico; leg. D. B. Cadien, 31 March 1972.
- 1 specimen, 9-135 m, Taboga Island, Panama Bay, Panama (80°35'N, 79°30'W); leg. E. Bergeron and J. H. McLean, 9 June 1965 (LACM 65-25).
- 3 specimens, intertidal, Cholla Bay, Sonora, Mexico; leg. C. Skoglund, 15 October 1978.

Nomenclatural Comments: Reported worldwide, *Lamellaria perspicua* was first recorded from the Pacific Ocean (southern Chile) by MARCUS (1959). Since that report, MARCUS & MARCUS (1967) assigned subspecific status to two variations of *L. perspicua* collected in Puerto Peñasco, Sonora, Mexico. Due to the geographical overlap of the two forms, and the number of specimens examined, separate status does not seem justifiable.

With further study, similarities between the *Lamellaria perspicua* described by MARCUS & MARCUS (1967) and *L. diegoensis* may prove them identical. Sufficient material was not available here to carry out such comparisons.

Description: I was unable to find or examine any living specimens of this species. The following description is

Explanation of Figures 16 to 19

Figure 16: *Lamellaria diegoensis*. Isla Vista, Santa Barbara County, California

Figure 17: *Lamellaria diegoensis*. Isla Vista, Santa Barbara County, California

Figure 18: *Marsenina stearnsii*. Diablo Canyon, San Luis Obispo County, California

Figure 19: *Marsenina stearnsii*. Diablo Canyon, San Luis Obispo County, California

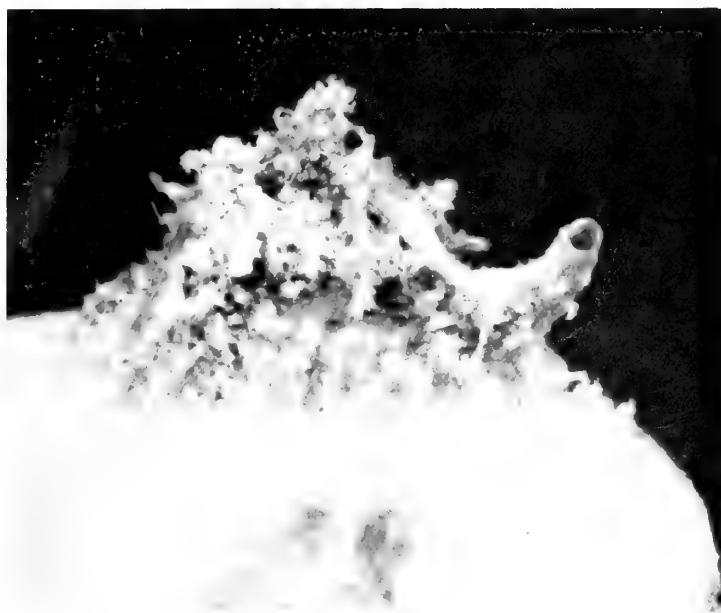


Figure 16



Figure 18

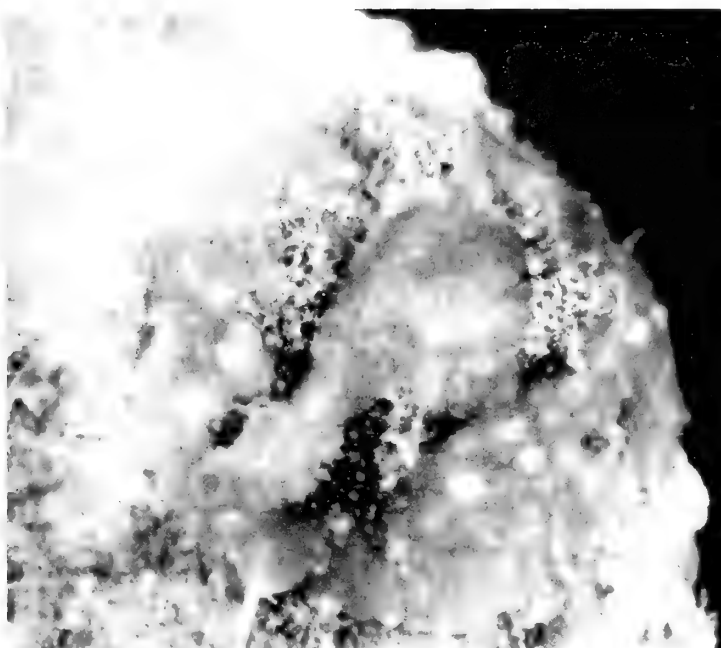


Figure 17

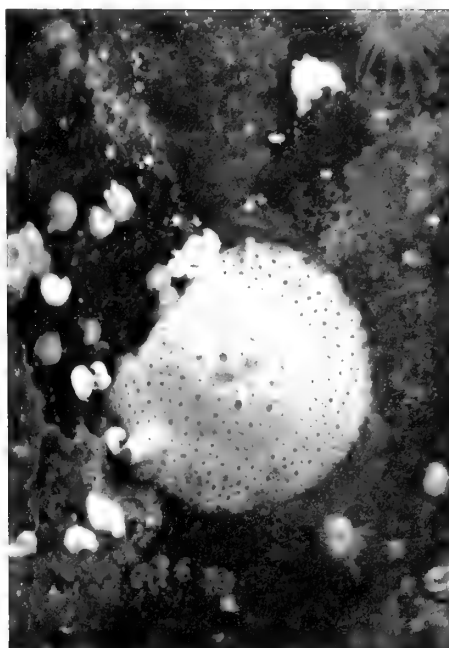


Figure 19

based upon 5 preserved specimens (listed above) and MARCUS & MARCUS (1967) for their animals collected in Puerto Peñasco, Sonora, Mexico.

External Morphology and Coloration: Lacking a dorsal pore or fissure (Figure 3), MARCUS & MARCUS (1967) describe it as more or less translucent, the male with the whitish hue, the female with the pinkish hue. Glandular inclusions of the skin opaque white in the male, vitreous in the female, the anterior border of the foot is opaque white. After preservation, the male exhibited black pigment spots standing out from the gray ground color, the female being more uniform. The sole of the foot is gray, the head lighter and the penis white. The specimen referred to as *Lamellaria perspicua mopsicolor* was a dark bluish gray. The cutaneous bosses in the mantle had dark centers, surrounded by lighter rings.

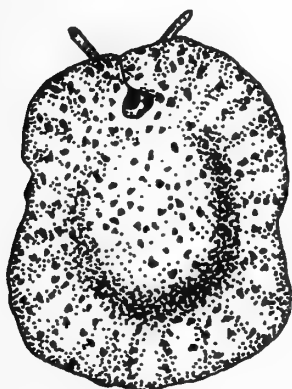


Figure 3

Drawing of living *Lamellaria perspicua*
(after MARCUS & MARCUS, 1967: 9)

The specimen collected by D. Cadien was reported to be yellowish-beige with brown markings, while alive. The C. Skoglund specimens were pinkish-brown with liver colored specks and small yellowish papillae. After preservation, the specimens faded to a translucent hue with brown and white specks. A color photograph of a European specimen appears in YONGE & THOMPSON (1976, plt. 9).

Shell: White, growth lines distinct. Apex prominent. MARCUS & MARCUS (1967) distinguish this species from

Lamellaria diegoensis by the absence of malleations on the shell surface. All of the D. Cadien, C. Skoglund and LACM specimens thought to be *L. perspicua* showed very slight malleations in the shell surface. Without the entire animal, it would appear that this species could not be recognized as *L. perspicua* from the shell alone.

Radula: (from MARCUS & MARCUS, 1967). Male has 60 rows, the female 79 rows of teeth. The left leg of the rachidian is slightly longer. This difference is more pronounced in the female. The male rachidian has 4-5 strong denticles on the right, 6-7 finer ones on the left; the female 5-8 and 8-10, respectively. The lateral tooth of the male has 4-8 strong inner and 7-12 finer outer denticles; the female 5-8 and 4-11, respectively. The specimen referred to as *Lamellaria perspicua mopsicolor* displayed 4-5 denticles on the right side of the rachidian only, while the laterals bore 4-6 coarse, sharp, inner and 8 smaller outer denticles (Figure 4).

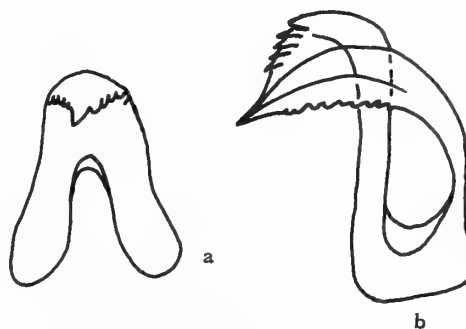


Figure 4

Radular teeth of *Lamellaria perspicua*

a - rachidian tooth

b - lateral tooth

The specimens I examined had 55 rows (DBC & LACM) and 41-45 rows (CS) of teeth. The rachidians bore 4-6 right, and 3-7 left denticles, the left set being finer. The laterals bore 3-5 strong inner, and 7-12 fine outer denticles. The left leg of the rachidian did not seem noticeably longer in any of the specimens.

This description bears a striking similarity to that of *Lamellaria diegoensis*, particularly because of similarity in shell surface textures and radular dentition (not previously described in *L. diegoensis*).

Size: MARCUS & MARCUS (1967) report their specimens to measure 15 by 10 mm and 18 by 19 mm, length by breadth. The largest specimens I examined were 18 by 15 mm (DBC) and 20 by 20 mm (LACM), preserved.

Distribution: Worldwide. Pacific Ocean: Magellanic region and southern Chile; Puerto Peñasco, Sonora, Mexico; Panama.

Lamellaria inflata (C. B. Adams, 1852)

(Figures 5, 6)

References and Synonymy:

- Stomatella inflata* C. B. ADAMS, 1852: 216, 440.
Lamellaria inflata (C. B. Adams). STRONG & HERTLEIN, 1939: 186, 236. TURNER, 1956: 56. SHASKY, 1961: 23. DUSHANE & POORMAN, 1967: 427. MARCUS & MARCUS, 1967: 148. DUSHANE & SPHON, 1968: 242. BERTSCH & SMITH, 1970: 172. KEEN, 1971: 483. ABBOTT, 1974: 145.

Material Examined:

- 1) 6 specimens, intertidal, Jarvis Island, Galapagos ($0^{\circ}25'S$, $90^{\circ}42'W$); *leg.* Ameripagos Expedition, 24 March 1971 (LACM 71-68)
- 2) 2 specimens, intertidal, Punta Alfaro, Isabela Island, Galapagos ($0^{\circ}25'20''S$, $90^{\circ}57'10''W$); *leg.* Ameripagos Expedition, 25 March 1971 (LACM 71-70)
- 3) 2 specimens, 15-30 m, Academy Bay, Santa Cruz Island, Galapagos ($0^{\circ}25'S$, $90^{\circ}15'38''W$); *leg.* Ameripagos Expedition, 18 March 1971 (LACM 71-55)
- 4) 1 specimen, Guaymas, Mexico; no *leg.*, no date (LACM HH-53)
- 5) 1 specimen, 18 m, Tenacatita Bay, Jalisco, Mexico; *leg.* G. Willett, no date (LACM A. 375)
- 6) 2 specimens, Puertecitos, Baja California ($30^{\circ}25'N$, $114^{\circ}38'W$); *leg.* R. Mucke, 26 December 1964 (LACM 67-15)
- 7) 2 specimens, 9-20 m, Banderas Bay, Jalisco, Mexico; *leg.* C. Snell and B. McMillen, 14 February 1967 (LACM 67-15)
- 8) 1 specimen, 4.5-20 m, Cuastecomate, Jalisco, Mexico ($19^{\circ}13'44''N$, $104^{\circ}44'53''W$); *leg.* J. McLean and P. Oringer, 13-21 October 1968 (LACM 68-41)
- 9) 1 specimen, 72-126 m, Guatulco Bay, Oaxaca, Mexico; *leg.* G. Willett, 7 March 1938 (LACM 38-9)
- 10) 1 specimen, Cape Tepoca, Lebos, Sonora, Mexico; *leg.* R. Poorman, March 1975 (identified from LACM color transparency)
- 11) 1 specimen, intertidal, San Luis Gonzaga, Baja California; *leg.* W. E. Harvey, 6 February 1966 (identified from color transparency)
- 12) 1 specimen, Cholla Bay, Pelican Point, Sonora, Mexico; 16 February 1969 (CAS)
- 13) 1 specimen, intertidal, Cholla Bay, Sonora, Mexico; *leg.* D. W. Taylor, 2 November 1968 (CAS)

Description: I was unable to examine any living animals of this species; however, preserved material was examined from LACM along with a series of color transparencies of living specimens from various contributors.

External Morphology and Coloration: Lacking a dorsal pore or fissure. Textured entirely by a series of small pores. Yellow in color, the mantle is marked by a brown saddle lying just posterior to the center of the dorsum, as well as a brown patch on either side of the anterior siphon (Figure 5). Neither the saddle nor the patches reach the margin of the dorsum. The coloration, although faded, is retained in the preserved animal.

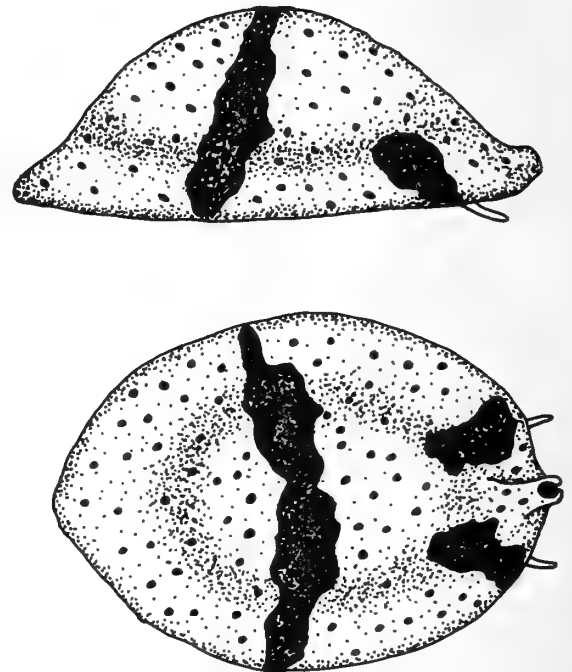


Figure 5

Drawing of *Lamellaria inflata* from color transparency of a live animal

Shell: White, thick, opaque. Fine irregular growth striae, without spiral striae. Suture well impressed. Similar in shape and character to *Marsenina stearnsii*. The reliance in the literature upon the description of the columellar side of the aperture being "abruptly arcuated" is, I think, unjustified. I found the angle of arcuation to be indistinguishable from that of the other species.

Radula: About 50 rows of teeth. The rachidian teeth are without any denticulation. The lateral has 3 strong inner denticles and 3-4 lesser outer denticles (Figure 6).



Figure 6

Radular teeth of *Lamellaria inflata*

a - rachidian tooth

b - lateral tooth

Size: From the specimens examined, this species seems to be of smaller size than the other species. The largest specimen measured 6 by 5 mm, length and breadth, respectively.

Distribution: Cape Tepoca, Puerto Lobos, Sonora, Mexico to Panama, as well as Bahia San Luis Gonzaga to La Paz, Baja California and the Galapagos Islands.

Lamellaria diegoensis Dall, 1885

(Figures 7, 8, 9, 16 and 17)

References and Synonymy:

- Lamellaria diegoensis* DALL, 1885: 538. DALL in ORCUTT, 1885: 538. OLDROYD, 1927: 738. WILLETT, 1939: 124. BURCH, 1946: 2. MORRIS, 1966: 76. MARCUS & MARCUS, 1967: 147. MCLEAN, 1969: 38. KEEN, 1971: 483. HUMAN, 1972: 28, 1973: 21. MCCLOSKEY, 1973: 157. BISHOP & BISHOP, 1973: 149. ABBOTT, 1974: 145.
- Marsenia diegoensis* (Dall). BERGH 1886(b): 13.
- Lamellaria orbiculata* Dall, 1871. MACGINITIE & MACGINITIE, 1949: 372. MARCUS & MARCUS, 1967: 147. KEEN, 1971: 483.

Material Examined:

- 1) 1 specimen, 15 m, Chace Reef, Lover's Point, Monterey Co., California; leg. Lloyd Gomez, 15 August 1969 (CAS)
- 2) 1 specimen, 12-15 m, Del Monte shale beds, Monterey Bay, California; leg. D. Powell, 7 March 1965 (CAS)
- 3) 1 specimen, 180 m off Soberanes Point, California; leg. D. D. Chivers, 20 July 1971 (CAS)
- 4) 1 specimen, Asilomar, Monterey Co., California; leg. G. McDonald, April 1971 (M71-4-33-1)
- 5) 1 specimen, intertidal, Garcia's Ranch, Cayucos, San Luis Obispo Co., California; leg. G. McDonald, 22 January 1970 (M70-1-22-3)
- 6) 1 specimen, Asilomar, Monterey Co., California; leg. G. McDonald, 14 October 1970 (M70-10-14-13)
- 7) 1 specimen, 18 m, Del Monte shale beds, Monterey Bay, California (36°37'N, 121°52.5'W); leg. J. H. McLean, 1960-62 (LACM 60-22)
- 8) 1 specimen, 200 ft., Los Angeles County Sanitation District-T3; leg. D. Cadien, 9 December 1976
- 9) 1 specimen, 135 m, Los Angeles County Sanitation District-T5; leg. D. Cadien, 14 December 1977
- 10) 1 specimen, 22.5 m, Palos Verdes, California; leg. D. Cadien, 11 October 1977
- 11) 1 specimen, Orange County; leg. D. Cadien, Summer 1974
- 12) 1 specimen, 135 m, Palos Verdes, California; leg. D. Cadien, 18 May 1977
- 13) 1 specimen, 21 m, Huntington Beach, RUNST #2, California; leg. D. Cadien, 6 February 1978
- 14) 1 specimen, 24 m, Engel's Bank, California; leg. D. Cadien, 8 February 1976
- 15) 7 specimens, 6 m, Isla Vista, Santa Barbara Co., California; leg. R. Henderson, 24 March 1977
- 16) 1 specimen, intertidal, Diablo Cove, San Luis Obispo Co., California; leg. L. L. Laurent, 23 September 1977
- 17) 1 specimen, 6 m, Seal Haul Out, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 23 September 1976
- 18) 1 specimen, Morro Bay, California; leg. D. W. Behrens, 7 February 1978
- 19) 1 specimen, Morro Bay, California; leg. D. W. Behrens, 8 March 1978
- 20) 1 specimen, 5 m, Intake Cove, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 27 April 1977
- 21) 1 specimen, intertidal, Seal Haul Out, Diablo Canyon, San Luis Obispo Co., California; leg. L. L. Laurent, 25 May 1978
- 22) 1 specimen, Isla Vista Beach, Santa Barbara Co., California; leg. R. Henderson, January 1978
- 23) 5 specimens, Punta Diggs, San Felipe, Baja California; leg. L. O. Miles, 15 April 1952 (CAS)

- 24) 1 specimen, Santa Barbara, California; leg. D. Olsen, 1961 (SBMNH 23600)
- 25) 1 specimen, Goleta Point, Santa Barbara, California; leg. D. Olsen, 6 December 1961 (SBMNH 23618)
- 26) 1 specimen, 4 mi so. of Gaviota, Santa Barbara County, California; leg. K. Newson, 11 November 1967 (SBMNH 24993)
- 27) 1 specimen, Boulder Beach, Summerland, Santa Barbara County, California; leg. S. Anderson, 26 June 1967 (SBMNH 24650)
- 28) 6 specimens, intertidal, Cholla Bay, Sonora, Mexico; leg. C. Skoglund, 15 October 1978

Description: EXTERNAL MORPHOLOGY AND COLORATION: Dorsal fissure or slit lacking. Mantle texture and color extremely variable, yet at the same time distinctive. Color

white through purple and brown; mottled, blotched and radially marked. Texture from smooth to velvety (Figure 7b) or papillated (Figure 7a) with branched projections. When present, mantle markings and papillations follow one of several specific formats: a dorsal saddle, as in *Lamellaria inflata*; a mid-dorsal horseshoe pattern with its opening situated anteriorly; or some variation of a radial pattern (Figure 8). Papillations usually white, brown and/or gray resembling tufts of hydroid or bryozoan growth (Figures 16 and 17). Underside of mantle speckled with yellow and white flecks. The foot is truncate anteriorly; rounded, posteriorly.

Shell: The most diagnostic feature of the shell is its mal-leated (hammered) surface texture. This character separates it from all other species. Columella without thickened callus.

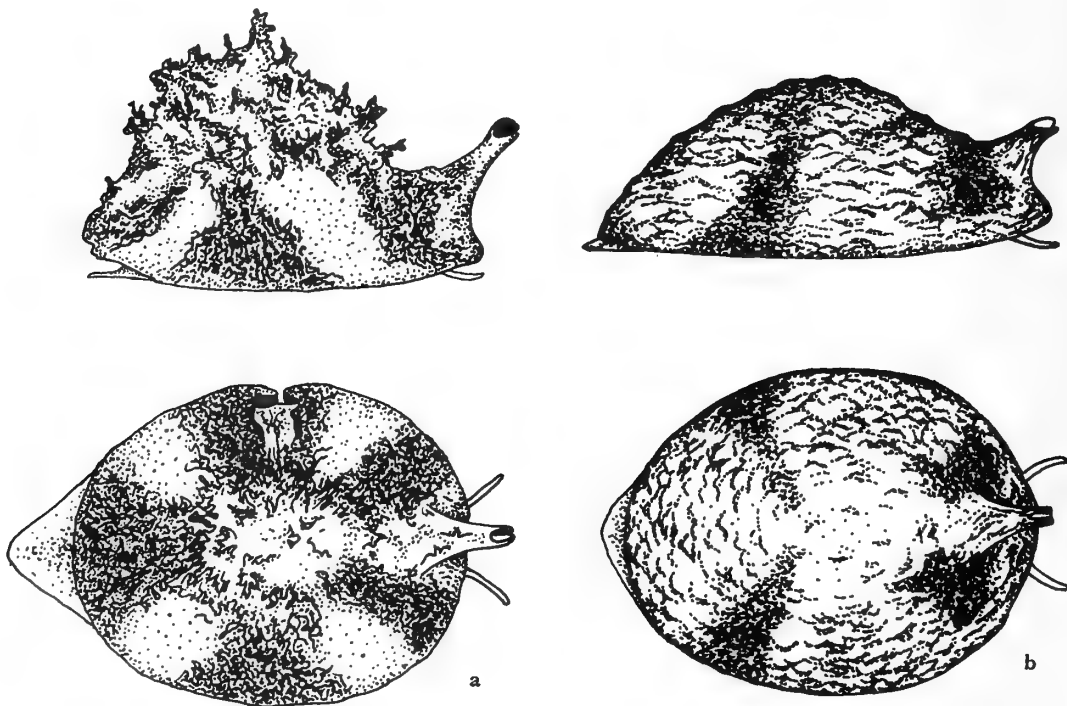


Figure 7

Drawing of *Lamellaria diegoensis*

- a) a highly papillose individual, Santa Barabara, 24 March 1977
- b) Specimen with low tubercles, Diablo Cove, San Luis Obispo County, 25 May 1978. Both drawn from color transparencies of the animals alive

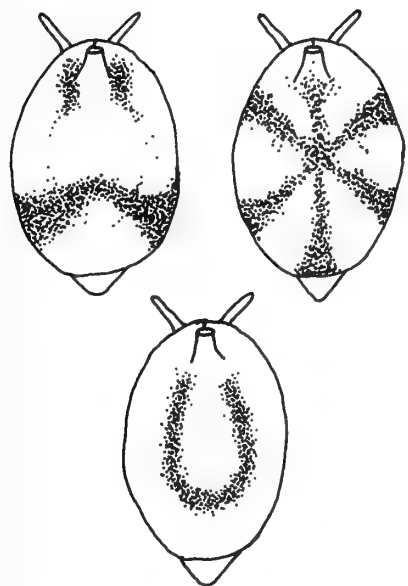


Figure 8

Common color pattern formats of *Lamellaria diegoensis*

Radula: Sixty rows of teeth. The rachidian is stout and nearly flat, not forming a hook, as in *L. perspicua* and

L. inflata (Figure 9b). It has 3-4 denticles on each side. The dentition on the lateral teeth begins farther from the tip of the tooth (Figure 9c). They have 4-5 outer denticles and 8-11 inner denticles. Lateral teeth overlap in an arrangement shown in Figure 9a.

Size: The largest of the Eastern Pacific lamellariids, it reaches 45 mm in both length and breadth.

Distribution: Moss Landing, California to Baja California and Sonora, Mexico. Intertidal to 139 m.

Marsenina J. E. Gray, 1850

The genus *Marsenina* in the Eastern Pacific is separated from the other lamellariid genera in that it is hermaphroditic (BERGH, 1853, 1886 a & b), and its mantle exhibits a dorsal fissure or pore and is retractile. Like *Marseniopsis*, the radula possesses marginal teeth (GRAY, 1850; BERGH, 1886 a&b).

Type Species: *Lamellaria proclita* Lovén, 1846 (by M) (= *Oxynoe? glabra* Couthouy, 1838)

Nomenclatural Comments: In the eastern Pacific, this genus is represented by two species: *Marsenina stearnsii* (Dall, 1871) and *Marsenina rhombica* (Dall, 1871). Originally, both were placed in *Lamellaria* by DALL (1871).

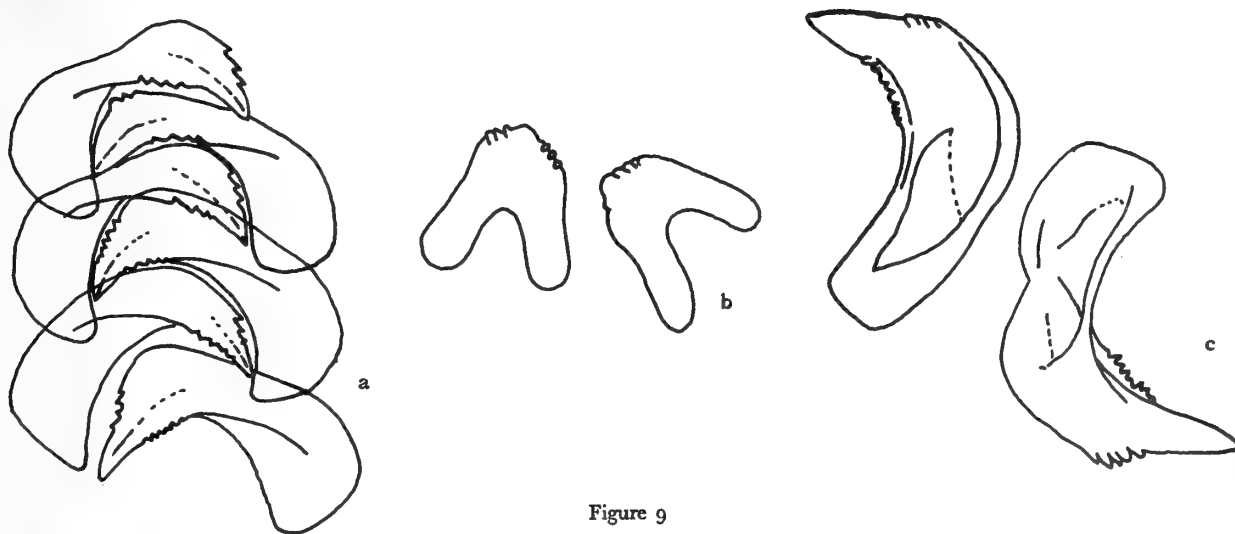


Figure 9

Radular teeth of *Lamellaria diegoensis*

- a) juxtaposition of lateral teeth (rachidians not shown)
 b) rachidian teeth
 c) lateral teeth

DALL in ORCUTT (1885) suggested placement of *L. rhombica* in *Marsenina* Gray, 1850, but failed to give any explanation for the reallocation. Had the radula been examined, *L. stearnsii* would have been placed there also.

The two species are indistinguishable based on Dall's original descriptions, which were based solely upon shell characteristics, and an examination of the types which are dry shells. Two morphologically different species do exist, however. Because of this, I am somewhat at a loss concerning which of the two names applies to the species found along this coast. Dall originally described a dorsal pore in the mantle of *Lamellaria rhombica*, but not in *L. stearnsii*. As previously mentioned, no poreless animal, aligned with this genus, has since been reported. GHISELIN (1964) was the first to note this discrepancy. In his report, he also provided photographs of a specimen with a dorsal pore, which he called *Lamellaria stearnsii*. Considering the distinct difference in the external morphology of the live animals, none of which had been reported until publication of Ghiselin's photographs, I propose that the precedent has been set for *Marsenina stearnsii*, leaving the name *M. rhombica* for the remaining species.

Marsenina stearnsii (Dall, 1871) *comb. nov.*

(Figures 10, 11, 18 and 19)

References and Synonymy:

- Lamellaria depressa* Dall, mss, 1866.
Lamellaria stearnsii DALL, 1871: 122. ORCUTT & DALL, 1885: 539. TRYON, 1886: 63. KEEF, 1892: 47. WILLETT, 1919: 26. OLDROYD, 1924: 164; 1927: 737. STRONG & HANNA, 1930: 19. ROGERS, 1936: 146. WILLETT, 1939: 124. BURCH, 1946: 2. SMITH & GORDON, 1948: 199. GHISELIN, 1964: 123. TALMADGE, 1966: 840. MARCUS & MARCUS, 1967: 147. BROOKSHIRE, 1968: 6. McCLOSKEY, 1973: 155. BISHOP & BISHOP, 1973: 149. ABBOTT, 1974: 146.
Marsenia stearnsii (Dall, 1871). BERGH, 1886(b): 13.
Lamellaria stearnsii Dall, 1871. THOMPSON, 1973: 75.
Lamellaria stearnsii orbiculata DALL, 1871: 122. ORCUTT & DALL, 1885: 539. OLDROYD, 1927: 738. BURCH, 1946: 2. ABBOTT, 1974: 146.
Marsenia orbiculata (Dall, 1871). BERGH, 1886(b): 13.
Lamellaria stearnsiana Dall, 1871. YATES, 1890: 44. HOWARD, 1972: 23.

Material Examined:

- 1) 7 specimens, Cape Arago Park, Oregon; no leg., 19 July 1947 (CAS)
- 2) 3 specimens, Yankee Point, Monterey Co., California; leg. A. G. Smith, 1955 (CAS)
- 3) 1 specimen, San Juan Island, Puget Sound, Washington; leg. L. Andrews, September 1964 (CAS)
- 4) 1 specimen, Portuguese Beach Park, Sonoma Co., California; leg. L. Andrews, 6 June 1963 (CAS)
- 5) 3 specimens, 9-12 m, Del Monte shale beds, Monterey Bay, California; leg. David Powell, 2 October 1964 (CAS)
- 6) 1 specimen, Pacific Grove, California; no leg., no date (CAS)
- 7) 4 specimens, Point Pinos, Pacific Grove, California; no leg., July 1910 (CAS)
- 8) 1 specimen, intertidal, Garcia's Ranch, Cayucos, San Luis Obispo Co., California; leg. G. McDonald, 22 January 1970 (M70-1-22-1)
- 9) 1 specimen, intertidal, Field's Ranch, San Luis Obispo Co., California; leg. G. McDonald, 29 May 1968 (M68-5-29-1)
- 10) 3 specimens, intertidal, Spooner's Cove, San Luis Obispo Co., California; leg. G. McDonald, 2 November 1971 (M71-11-2-5)
- 11) 7 specimens, intertidal, Ethelda Bay, Hecate Strait, British Columbia (52°58.2'N, 129°31.2'W); leg. D. B. Quayle and F. R. Bernard, 22 October 1968 (LACM 68-74)
- 12) 5 specimens, 6 m, Intake Cove, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 20 September 1976
- 13) 1 specimen, Diablo Cove, San Luis Obispo Co., California; leg. J. L. Kelly, 29 September 1977
- 14) 1 specimen, 6 m, Intake Cove, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 15 May 1978
- 15) 4 specimens, 6 m, Seal Haul Out, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 20 September 1976
- 16) 3 specimens, 8 m, Seal Haul Out, Diablo Canyon, San Luis Obispo Co., California; leg. D. W. Behrens, 27 April 1978

Explanation of Figures 20 to 23

Figure 20: *Marsenina rhombica*. Point Piedras Blancas, San Luis Obispo County, California 30 mm

Figure 21: Two *Marsenina rhombica*. Point Piedras Blancas, San Luis Obispo County, California 23 and 35 mm, respectively

Figure 22: *Marseniopsis sharonae*. Morro Bay, California, substrate, *Botrylloides* sp. 15 mm

Figure 23: *Marseniopsis sharonae*. Morro Bay, California, substrate, *Botrylloides* sp. 15 mm



Figure 20



Figure 22



Figure 21



Figure 23

Description: **EXTERNAL MORPHOLOGY AND COLORATION:** Mantle with a dorsal slit, pore or fissure which may be retracted to expose the shell (Figure 10). Mantle smooth. Color white to pinkish-white with a pattern of evenly-spaced small pores (Figures 18 & 19). These pores may be seen from beneath, through the mantle. Where the shell is exposed, internal organs show through the shell and are salmon colored. GHISELIN (1964) published black and white photographs of the species, on and off its tunicate substrate.

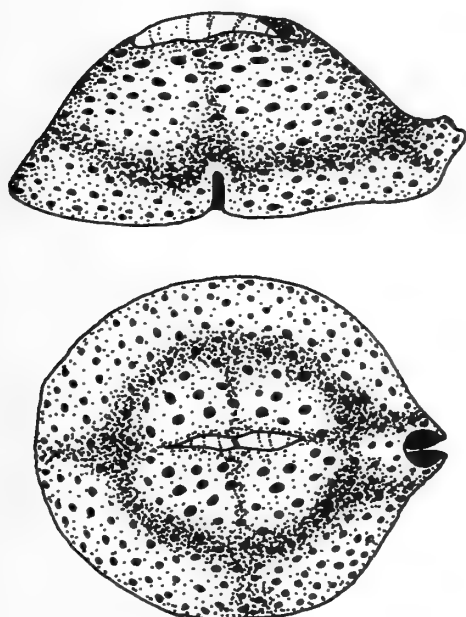


Figure 10

Drawing of *Marsenina stearnsii* from color transparency of live animal. Diablo Canyon, San Luis Obispo County, California

Shell: Smooth, thick, opaque white. Indistinguishable from those of *Lamellaria inflata* and *Marsenina rhombica*. Growth lines even and smooth. DALL (1871) described the characteristic of microscopic fine revolving striulae which later (1885) he described as distinctive. At my request, Dr. Harold Rehder, USNM, examined the holotype and reports to me that he was unable to find such a character in the shell surface. I too, have yet to find this character in any North Eastern Pacific lamellariid shell.

Radula: Differs from *Lamellaria* by possessing marginal teeth (Figure 11a). The rachidian teeth are truncate pos-

teriorly, hooked anteriorly with none or one denticle flanking the medium spur. In plane view, they appear nearly square (Figure 11b). The lateral teeth are similar to the rachidian in dentition. There are two long, thin, hook-shaped marginal teeth, as in *Marseniopsis*. Each marginal tooth has one denticle situated to the outside of the pair of teeth (Figure 11d). Not included in the original description, the radula agrees closely with that described for *Marsenina* in GRAY (1850), and later in BERGH (1886b).

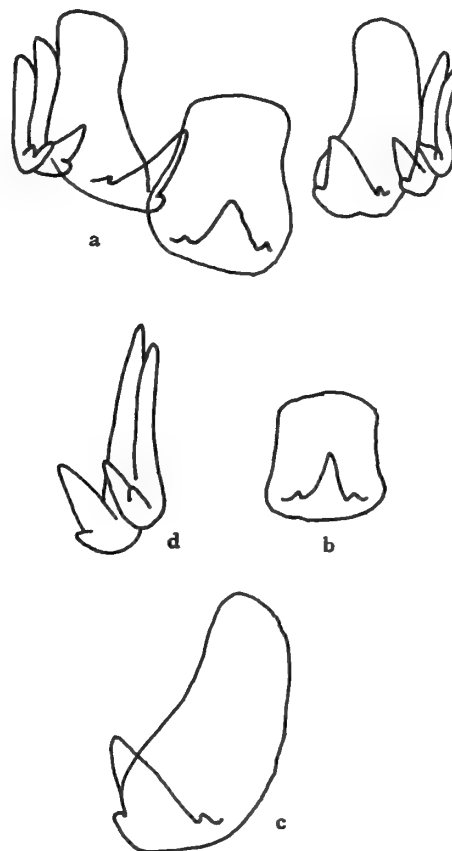


Figure 11

Radular teeth of *Marsenina stearnsii* and *Marsenina rhombica*
 a) juxtaposition of radular teeth b) rachidian tooth
 c) lateral teeth d) pair of marginal teeth

Size: Moderate, reaching 18 by 16 mm in length and breadth.

Distribution: British Columbia, Canada to San Diego, California. Its occurrence at Maria Madre Island, Mexico

(STRONG & HANNA, 1930) is questionable. Intertidal to 8 m subtidally.

Marsenina rhombica (Dall, 1871)

(Figures 11, 12, 20 and 21)

References and Synonymy:

- Lamellaria rhombica* Dall, 1871: 122. DALL in ORCUTT, 1885: 539. OLDROYD, 1924: 164; 1927: 137. ROGERS, 1936: 147. WILLETT, 1939: 124. BURCH, 1946: 2. SMITH & GORDON, 1948: 199. GHISELIN, 1964: 123. MARCUS & MARCUS, 1967: 147. McCLOSKEY, 1973: 155. ABBOTT, 1974: 145.
Marsenina rhombica (Dall, 1871). ORCUTT & DALL, 1885: 539. BERGH, 1886(b): 14. ROGERS, 1951: 492. LAROCQUE, 1953: 157.

Material Examined:

- 1) 1 specimen, Carmel Point, Monterey Co., California; leg. G. McDonald, 2 December 1971 (M71-12-2-4)
- 2) 2 specimens, Carmel Point, Monterey Co., California; leg. G. McDonald, 3 November 1971 (M71-11-3-3 & 4)
- 3) 1 specimen, Spooner's Cove, San Luis Obispo Co., California; leg. G. McDonald, 2 November 1971 (M71-11-2-5)
- 4) 2 specimens, 1½-4½ m, Halibut Point, Sitka Sound, Baranof Island, Alaska (56°06'N, 135°24'W); leg. J. H. McLean, 25 and 26 July 1973 (LACM 73-13)
- 5) 4 specimens, intertidal, Ethelda Bay, Hecate Strait, British Columbia (52°58.2'N, 129°31.2'W); leg. D. B. Quayle & F. R. Bernard, 22 October 1968 (LACM 68-74)
- 6) 1 specimen, Shelter Lane, California; no leg., 30-31 May 1946 (CAS)
- 7) 1 specimen, intertidal, Point Piedras Blancas, San Luis Obispo Co., California; leg. D. W. Behrens, 20 November 1976
- 8) 2 specimens, intertidal, Point Piedras Blancas, San Luis Obispo Co., California; leg. D. W. Behrens, 11 November 1977
- 9) 5 specimens, intertidal, Point Piedras Blancas, San Luis Obispo Co., California; leg. R. Henderson, 13 November 1977
- 10) 1 specimen, intertidal, Point Piedras Blancas, San Luis Obispo Co., California; leg. D. W. Behrens & S. Anderson, 30 December 1978
- 11) 2 specimens, 6 to 13.5 m, Zaikof, Montague Island, Alaska; leg. R. Fay, 9 September 1978 (RH)

Description: EXTERNAL MORPHOLOGY AND COLORATION: As in *Marsenina stearnsii*, a dorsal pore in the mantle exposes the shell (Figure 12). Mantle texture varies from smooth to warty. Color is variable, translucent to gray or yellow and orange with various degrees of spotting, speckling or blotching (Figures 20 & 21). Points of color appear to penetrate deep into the mantle, as bosses. Several specimens had a black swath posteriorly adjacent to the dorsal pore.

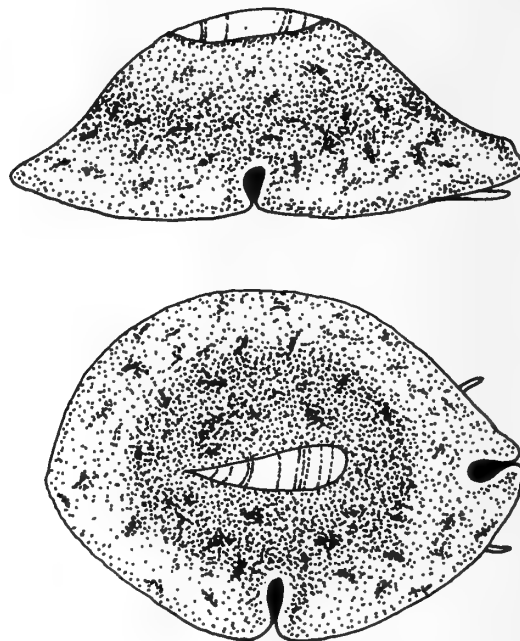


Figure 12

Drawing of *Marsenina rhombica* from color transparency of live animal. Point Piedras Blancas, San Luis Obispo County, California

Shell: Generally indistinguishable from *Marsenina stearnsii*. A very thick, strong growth mark was observed in several specimens. This feature was not seen in any *M. stearnsii*.

Radula: Not distinguishable from *Marsenina stearnsii*. See description above (Figure 11).

Size: Larger than *Marsenina stearnsii*, reaching 40 x 35 mm in length and breadth.

Distribution: Montague Island, Alaska to Diablo Cove, San Luis Obispo County, California. Intertidal to 60 meters subtidally.

Marseniopsis Bergh, 1886

The genus *Marseniopsis* in the Eastern Pacific can be characterized by separate sexes, naticoid shell, hexahedral body shape and a distinctive radula.

Type Species: *Marseniopsis pacifica* Bergh, 1886 (*vide* WENZ, 1938).

Marseniopsis sharonae (Willett, 1939)

(Figures 13, 14, 15, 22 and 23)

References and Synonymy:

- Lamellaria sharoni* WILLETT, 1939: 123.
Lamellaria sharonae Willett, 1939. BURCH, 1946: 1. CATE & CATE, 1962: 91. DUSHANE & SPHON, 1968: 235, 242. MCLEAN, 1969: 39. KEEN, 1971: 485. BISHOP & BISHOP, 1973: 149. ABBOTT, 1974: 145.
Lamellaria sp. MACGINITIE & MACGINITIE, 1949: 115.
Marseniopsis sharonae (Willett, 1939). SPHON, 1975: 95.

Material Examined:

- 1) 2 specimens, Morro Bay State Park, Morro Bay, San Luis Obispo Co., California; *leg.* R. A. Roller, 2 February 1968 (M68-2-2-1)
- 2) 1 specimen, intertidal, Puerto Peñasco, Sonora, Mexico; *leg.* D. Cadien, 1 April 1972
- 3) 1 specimen, 20 m, Oyster Point, San Mateo Co., San Francisco Bay, California; *leg.* D. D. Chivers, 17 August 1971 (CAS)
- 4) 29 specimens, 5 m, Morro Bay, California; *leg.* D. W. Behrens, 10 February 1977
- 5) 15 specimens, 1.5 m, Morro Bay, California; *leg.* D. W. Behrens, 20 April 1977
- 6) 19 specimens, 3 m, Morro Bay, California; *leg.* D. W. Behrens, 27 July 1977
- 7) 9 specimens, 3 m, Morro Bay, California; *leg.* D. W. Behrens, 18 August 1977
- 8) 13 specimens, 3 m, Morro Bay, California; *leg.* D. W. Behrens, 7 September 1977
- 9) 21 specimens, 1.5 m, Morro Bay, California; *leg.* D. W. Behrens, 24 October 1977

Nomenclatural Comments: Its original placement in *Lamellaria* by Willett was apparently done hesitantly, as reported by BURCH (1946). SPHON (1975) later reassigned it to the genus *Marseniopsis* without data or basis given for the reallocation. However, on the basis of radular morphology (BERGH, 1886b), I concur with Sphon's generic placement.

Description: EXTERNAL MORPHOLOGY AND COLORATION:

The shape of the mantle is its most diagnostic character (Figures 13, 22 and 23). Lacking a dorsal fissure or slit, it is divided into six areas by low ridges that commence from a raised hexagonal area in the center of the dorsum. In the preserved state, the shape remains as a tight six-sided bead. Color in life is highly variable, white through red, purple and brown. The ridges are ornamented with a series of specks and irregular spots. A single spot is usually found in the center of the dorsal hexagon and on each side. As a rule, light colored specimens have dark spotting while darker specimens are ornamented with light spotting. A color photograph appears in KEEN (1971, plt. XVI).

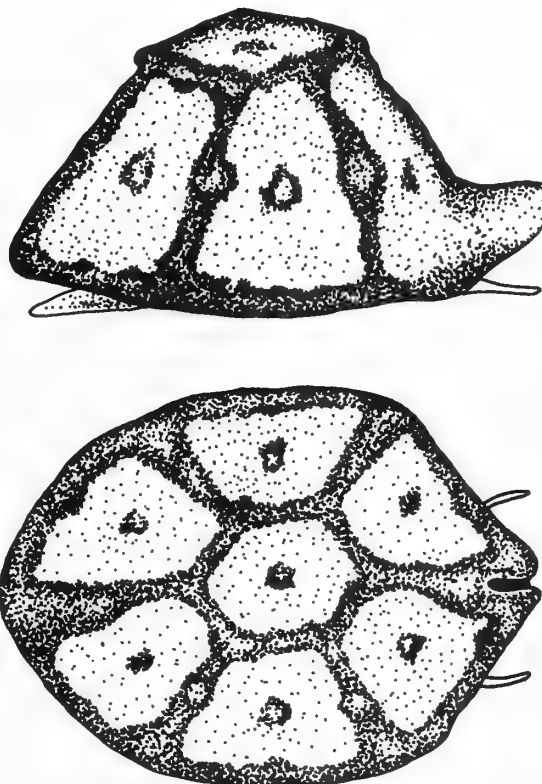


Figure 13

Drawing of *Marseniopsis sharonae* from color transparency of live animal
 Morro Bay, California

Shell: Naticoid in form, much more so than any other lamelliariid (Figure 14). Very thin, transparent. Columella brown. Pinkish periostracum.

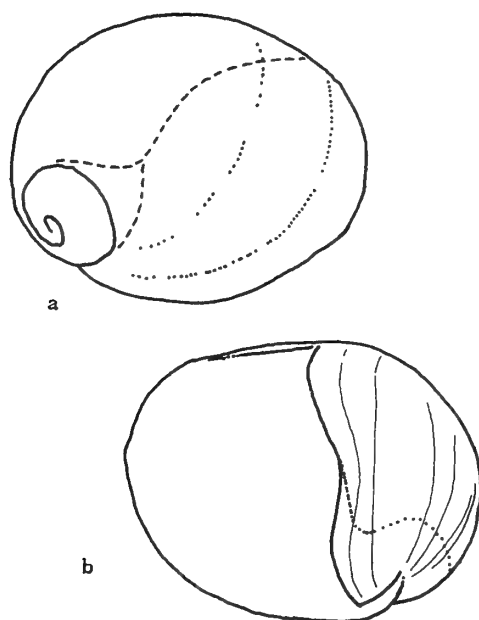


Figure 14

Drawing of the shell of *Marseniopsis sharonae*, 8 mm
a) dorsal view b) ventral view

Radula: Distinctive in dentition from other lamelliariids, 2.1.1.1.2 (Figure 15). The rachidian teeth are not forked posteriorly as in *Lamellaria*, but truncate. The rachidian dentition is best described as having five strong terminal denticles. Two denticles are lateral to and slightly behind the center denticle. The laterals are similar to the rachidian in strength, having 3 equal strong terminal denticles and two weak outer denticles. There are two marginal teeth in the radula, as in *Marsenina*. They are long, thin and forked at their anterior end. The outer tooth appears to cross over the inner tooth. This aligns the denticles of each in a lateral series with each other and those of the adjacent lateral tooth (Figure 15a). Such a radula agrees closely with that described in *Marseniopsis* in BERGH (1886a & b).

Size: Of moderate size, it reaches 13 mm in length and breadth.



Figure 15

Radular teeth of *Marseniopsis sharonae*

- a) juxtaposition of radular teeth b) rachidian tooth
c) lateral tooth d) pair of marginal teeth

Distribution: Coos Bay, Oregon (personal communication, James Lance, La Jolla, California) to Puerto Peñasco, Sonora, Mexico, and Bahia San Luis Gonzaga, Baja California. Intertidal to shallow (5 m) subtidal.

MIS-ALLOCATED SPECIES

Other mollusk species have, on occasion, been incorrectly allocated to Lamelliariidae, most notably the Pleurobranchidae. In the North Eastern Pacific, OLDROYD (1927), WILLETT (1939) and ABBOTT (1974) refer to a *Lamellaria digueti* Rochebrune (1895). Originally *Pleurobranchus digueti*, it was allotted to *Lamellaria* by DALL (1871). BURCH (1946) was the first to note the misplace-

ment. MARCUS & MARCUS (1967) report this allocation to be untenable.

Key to the Species of the Lamellariidae of the North Eastern Pacific (based on mantle characteristics)

1. Mantle with dorsal slit, pore or fissure, which may expose the shell when the mantle is retracted..... 2
 - Mantle whole, without a dorsal pore or fissure..... 3
2. Mantle smooth, white to pinkish white, with a pattern of evenly spaced transparent acid glands resembling small pores.....
 -*Marsenina stearnsii* (Dall, 1871)
- Mantle smooth to warty. Color variable, translucent or grey to yellow and orange, with or without various degrees of spotting or blotches.....
 -*Marsenina rhombica* (Dall, 1871)
3. Mantle divided into six areas by low ridges that commence from a raised hexagon in the center of the dorsum. Color variable, white through orange, red, purple and brown. A single spot in center of dorsal hexagon and on each side.....
 -*Marseniopsis sharonae* (Willett, 1939)
- Mantle not divided into six areas by low ridges forming a raised hexagon..... 4
4. Underside of mantle with white or yellow specks. Mantle smooth to velvety or papillated. Color variable.....*Lamellaria diegoensis* Dall, 1885
- Underside of mantle without white or yellow specks..... 5
5. Mantle smooth, opaque yellow, with a brown saddle across dorsum, as well as a brown patch on either side of the anterior siphon. Remainder of mantle covered with a pattern of evenly spaced pores.....*Lamellaria inflata* (C. B. Adams, 1852)
- Mantle translucent, white, yellow or pinkish brown. Glandular inclusions on the skin glassy or white to brown.....*Lamellaria perspicua* (Linnaeus, 1758)

NATURAL HISTORY AND PROTECTIVE RESEMBLANCE

Substrate preference and the question of protective resemblance have received a great deal of discussion in the

literature. HERDMAN (1893) and ANKEL (1935) reported an association between *Lamellaria perspicua* and the Atlantic ascidian *Didemnum candidum* (= *Leptoclinum maculatum*) which they considered as protective to the lamellariid. THOMPSON (1973, 1976) collected *Lamellaria* from southern Britain, none of which resembled an ascidian host, but instead resembled other substrata. He found *Lamellaria latens* which resembled the hard marine substratum upon which it was collected and *L. perspicua* which resembled an assemblage of barnacles. Of the latter, two specimens were collected at Helford, Cornwall, with barnacle-like markings on their dorsa. So life-like was the resemblance, a hand lens was required to show otherwise. This fascinating phenomenon is documented with color photographs in YONGE & THOMPSON (1976).

On the Pacific Coast at Corona del Mar, California, MACGINITIE & MACGINITIE (1949) report an unidentified yellow lamellariid feeding upon the yellow sponge, *Lissodendoryx noxiosa* and a brick-red lamellariid (*Marseniopsis sharonae*, their figure 200) feeding upon a sponge of the same color. At Puerto Peñasco, Sonora, Mexico, they report *Lamellaria orbiculata* (probably *L. diegoensis*) as occurring on the underside of rocks encrusted with either a white sponge or white tunicate, which it closely resembles. GHISELIN (1964) discusses the morphological and behavioral relationships of the resemblance of *Marsenina stearnsii* (= *Lamellaria stearnsii*) to the compound ascidian, *Trididemnum opacum* (Ritter, 1907) upon which it lives. McCLOSKEY (1973) concurs with Ghiselin that *Marsenina rhombica* (= *Lamellaria rhombica*) also resembles a tunicate colony, but occurs on other substrata as well. McCloskey collected his specimens on the solitary tunicate *Ascidia paratropa* (Huntsman, 1912).

Although I collected many animals on barren rock surfaces, my observations support the contention that all lamellariid species are, for the most part, tunicate-substrate specific. Of the genus *Lamellaria*, only *L. diegoensis* was observed in the field. Excluding the 8 animals collected on barren rock, 15 specimens were collected on *Aplidium* sp., *Cystodytes lobatus* (Ritter, 1900), *Eugyra* sp., *Polyclinum planum* (Ritter & Forsyth, 1917) and *Trididemnum opacum*. Two specimens found on *T. opacum* were highly cryptic, white animals marked similarly to *Marsenina stearnsii*. A single specimen found in beach wash algae on Isla Vista Beach, Santa Barbara County, California, was marked with two pink coralline algae-colored areas on a brown background; this observation is most likely incidental and inconclusive.

Seven individuals of *Lamellaria diegoensis* collected from a single salmon-colored colony of *Aplidium* near Isla Vista Beach, California, although cryptic, exhibited 7

separate color and texture phases. Marked typically, individuals included yellow, orange, brown, lavender and gray color regimes.

I found *Marsenina stearnsii* to possess the very strict substrate specificity and resemblance reported by GHISELIN (1964). All specimens were collected on *Trididemnum opacum*, and were almost indistinguishable from the tunic of the host.

Marsenina rhombica was collected from several tunicate species. In each case, the gastropod's color and texture closely resembled the host substrate. Those tunicate hosts identified included *Aplidium* sp., *Ascidia* sp. and *Cystodytes* sp.

Marseniopsis sharonae was found only on *Botryoloides* sp., an orange, quiet-water species. Despite the wide color range of *M. sharonae*, it was often difficult to locate individuals sunken in the surface or in folds of this encrusting tunicate species.

The exact substrate preferences for *Lamellaria perspicua* and *L. inflata* are unknown; however, color notes accompanying specimens, when available, report the animals closely resembled their tunicate host.

PREDATOR DETERRENT

AND EPIFAUNAL RELATIONSHIPS

Some members of the Lamellariidae possess a predator deterrent in the form of acid secretions from glands in the mantle (THOMPSON 1960, 1969, 1976; YONGE & THOMPSON 1976). THOMPSON (1960) studied such secretions in *Lamellaria perspicua* from the Atlantic. This feature has not been investigated in any other Pacific species. YONGE & THOMPSON (*op. cit.*) presume that the acid secretion functions to dissuade a sharp-sighted predator which has not been fooled by the snail's protective resemblance.

In the laboratory, I have observed the opisthobranchs *Triopha catalinae* (Cooper, 1863) and *Hermisenda crassicornis* (Eschscholtz, 1831) to retreat hastily from the contact with the mantle of *Marsenina rhombica*. This contact-retreat behavior was repeated several times by the same animal.

Another Pacific species of lamellariid shows no such deterrent, and in contrast, allows a variety of fouling organisms to attach to its mantle. Until this study, I was aware of only two examples of molluscan mantle epifauna: these were the growth of barnacles on the mantle of the keyhole limpet, *Megathura crenulata* (John Carter, Lockheed Center for Marine Research (LCMR), personal communication), and hydroids on the mantle of the gum-

boot chiton, *Cryptochiton stelleri* (Douglas Hunt, LCMR, personal communication). I am not aware, however, of any published reports on such associations on living meso-gastropod mantles.

I noted epifaunal associations on *Marseniopsis sharonae* in Morro Bay. In 9 instances, I observed live barnacles, *Balanus* sp., attached to the living non-retractile mantle tissue of the host. The barnacles measured up to 1.5 mm diameter. A minute hydroid, *Plumularia* sp., was found on 6 specimens. Like the barnacles, the hydroids were firmly attached to the mantle tissue.

The third species growing on mantle tissue was the scud, *Corophium* sp. These were found with their secreted mucous tubes attached to the mantles of five specimens. On the most heavily encrusted specimen, the *Corophium* mat covered nearly one-half of the exposed mantle. A subsequent association, most certainly due to the scud encrustation, was the occurrence of the boring clam *Hiatella arctica*. Two to 4 individuals were found within the mucous mat encrusting all 5 lamellariids. *Hiatella* and *Balanus* were also found living on the tunic of the tunicate *Botryoloides* sp. on which the *Marseniopsis* were collected.

ACKNOWLEDGMENTS

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Predation by the Prosobranch Mollusk

Lamellaria diegoensis on *Cystodytes lobatus*, a Colonial Ascidian

BY

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(1 Text figure)

INTRODUCTION

THE LAMELLARIID GASTROPODS are highly specialized for predation on ascidians (HERDMAN, 1893; FRETTER & GRAHAM, 1962; GHISELIN, 1964). All the lamellariids are cryptically colored; some resemble their prey while others resemble the general substrate of their surroundings (THOMPSON, 1973). Their overall biology is poorly understood, however, because collections have been of only one or a few specimens at a time, and lengthy studies have not been carried out. The present paper describes the predator-prey relationship between *Lamellaria diegoensis* Dall, 1885, and the compound ascidian *Cystodytes lobatus* (Ritter, 1900). The results of several feeding experiments and calorimetric measurements of the ascidian colonies and mollusk feces are included, with a partial energy budget for *L. diegoensis* computed from these data. All observations and experiments were carried out on a single *L. diegoensis* because although *C. lobatus* is very common in the low intertidal and subtidal zones in central California, only one *L. diegoensis* was collected despite a concerted effort to find more over a six-month period. In spite of the drawbacks of the small sample size, this work was carried out because it may well be that the only way we shall ever gain a fairly comprehensive knowledge of the biology of the lamellariids is from the compilation of many separate studies.

METHODS

One *Lamellaria diegoensis* was collected on March 7, 1978, on a piece of *Cystodytes lobatus* colony from the low

intertidal zone during a -18 cm tide at Pt. Pinos, Pacific Grove, California. The piece of *C. lobatus* colony and additional colonies were maintained in an aquarium with running sea water at the Hopkins Marine Station; the mollusk was not actually observed on the colonies until March 23, even though the colonies had been examined daily in conjunction with another study (LAMBERT, 1979).

The mollusk was maintained solely on a diet of *C. lobatus* from March 7 until August 31, 1978. For most of this period it was kept cool on the water table in a Pyrex baking dish loosely covered with black plastic. This partial darkness was provided because like *Lamellaria stearnsii* Dall, 1871, studied by GHISELIN (1964), *L. diegoensis* reacted strongly and negatively to bright light. The water was changed once a day and a new piece of ascidian colony offered every two to three days.

During July and August, a total of 15 daily fecal pellet counts, wet weights and dry weights were made with the aim of ultimately using these values to determine the amount of prey consumed and therefore the calories ingested. To this end, pieces of fresh ascidian colonies and the *Lamellaria* fecal pellets were dried to constant weight at 55°C (Table 1), and the caloric content determined using a Parr model 1411 semimicro bomb calorimeter (Table 2). Ash determinations were made with a muffle furnace for the *C. lobatus* colonies; there were not enough mollusk feces for this procedure, so the percent ash given in Table 2 was calculated from the bomb residue. In both cases the ash content has been corrected for CaCO₃ endothermy according to PAINE (1966, 1971) because of the large quantity of ascidian spicules. No acid corrections were made because of the large amount of naturally occurring acid in these animals.

Table 1

Wet and dry weights (mg) of *Cystodytes lobatus* colonies and *Lamellaria diegoensis* fecal pellets.

<i>Cystodytes lobatus</i>			<i>Lamellaria diegoensis</i> fecal pellets/24 hrs				
Wet	Dry	Ratio	Date	# Pellets	Wet	Dry	Ratio
2877	294.5	0.102	7/13/78	207	88.0	22.8	0.259
3277	318.5	0.097	7/14	162	84.9	23.3	0.274
3393	327.0	0.096	7/17	147	80.6	18.3	0.227
2786	253.0	0.091	7/20	128	58.9	11.8	0.200
3573	331.5	0.093	7/26	186	88.7	26.1	0.294
3462	297.0	0.086	8/1	134	81.4	18.9	0.232
3210	284.5	0.089	8/6	172	95.1	22.6	0.238
3299	275.0	0.083	8/10	104	49.4	12.6	0.255
3261	290.4	0.089	8/11	150	81.3	19.5	0.240
3418	284.6	0.083	8/14	112	62.5	15.9	0.254
			8/15	177	87.1	21.5	0.247
\bar{x} 3256	295.6	0.091	8/16	165	84.0	17.6	0.210
		± 0.006	8/19	132	62.6	13.1	0.209
			8/20	136	64.8	13.1	0.202
			8/21	162	78.9	12.1	0.153
				152	76.5	17.9	0.233 \bar{x}
				± 28	± 13.4	± 4.7	± 0.035

Table 2

Average energy values (calories/g ash-free dry wt) of *Cystodytes lobatus* colonies and *Lamellaria diegoensis* fecal pellets.

	\bar{x} cal g ⁻¹ ash-free dry wt (\pm SD)	# det.	% ash (bomb det.)	% ash (muffle furnace det.)	# det.
<i>Cystodytes lobatus</i> whole colonies	3679 \pm 244	7	62.9	63.3	3
<i>Lamellaria diegoensis</i> fecal pellets	5578 \pm 107	5	78.8	—	

RESULTS AND DISCUSSION

EXTERNAL MORPHOLOGY OF *Lamellaria diegoensis*

The following description of the living mollusk adds to BEHRENS' (1980) redescription (this issue) of this species. The shell was completely internal, with no opening on the mid-dorsal mantle surface to expose the shell. The pale pink mantle glistened with many shiny refractile spots. Flecks of black pigment were scattered everywhere, but they were especially numerous on the variable-sized contractile tubercles, which were largest mid-dorsally. Small tubercles extended right to the mantle edges and were also pale pink. Orange pigment could be seen inside some of the largest tubercles; its color closely matched the orange yolk of tadpole larvae developing in the ascidian

colonies. White material was concentrated at the base of some of the tubercles; it resembled the white calcareous spicules that occur in large numbers in *Cystodytes lobatus* and form sacs that surround each zooid abdomen (LAMBERT, 1979). Many yellow pigment spots occurred on the inside of the mantle and on the top and bottom of the foot that were not visible in a dorsal view. The foot, visible posteriorly only when the animal was moving, also had a large number of red pigment spots. Like all the lamellariids (FRETTER & GRAHAM, 1962; THOMPSON, 1969), the mantle contained numerous acid glands that produced sulfuric acid, as indicated by barium sulfate precipitation when barium chloride was added to a drop of mantle fluid. In this respect it again resembled its prey, for the test of *C. lobatus* is packed with numerous sulfuric acid filled

bladder cells (Abbott & Newberry, in press) 35 to 50 μm in diameter (LAMBERT, 1979).

The anterior end of the mantle formed a siphon that was usually greatly extended when the mollusk was moving. When it was resting or feeding on *Cystodytes*, its siphon and dorsal tubercles were considerably shortened and its body much flattened. The lateral mantle edges became spread out, giving the animal an almost circular

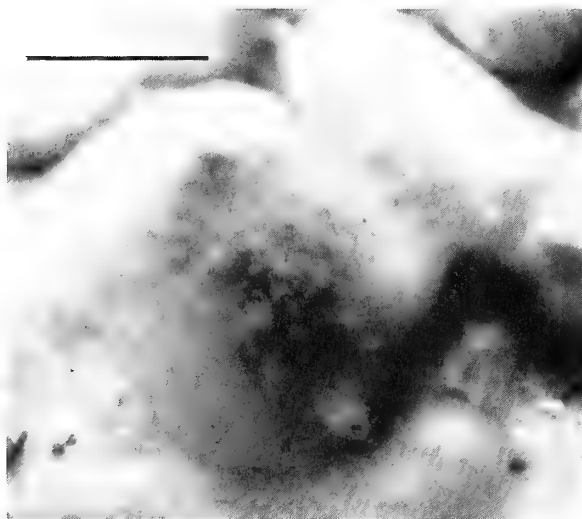


Figure 1

Lamellaria diegoensis at rest on a colony of *Cystodytes lobatus*
scale bar 2 cm

outline (Figure 1). The mantle edges became thin, translucent and nearly colorless, blending in with the bladder cell filled tunic of *C. lobatus* so well that the outline of the mollusk was difficult to distinguish.

FEEDING ON *Cystodytes lobatus*

Cystodytes lobatus occurs primarily in two color forms, translucent white and pale pink. The *Lamellaria diegoensis* blended somewhat better on the pink colonies and was originally collected on a pink colony but showed no feeding preferences between the two color types. The method of feeding has been described in detail by FRETTER & GRAHAM (1962): The animal rasps through the ascidian test and sucks up the zooids, leaving a hole with scalloped edges. In *Cystodytes* the zooid abdomens are surrounded by spicular sacs made up of closely overlapping disc-shaped calcium carbonate spicules. Inserting a fine probe into the tunic ruptures some of the acid-filled bladder cell membranes beyond the spicular sac, resulting in immediate dissolution of nearby spicules and release of CO_2 bubbles. The *L. diegoensis* ate right through the tunic, ingesting large numbers of spicules along with the zooids, and many of the spicules appeared in the feces almost undamaged in appearance, indicating that the mollusk was somehow able to neutralize the bladder cell contents quickly. The feces were either white or pink depending on the color of the tunicate colony being eaten. The feces had a striped appearance, with layers of spicules and tunic material alternating along the length of the pellet. This might reflect the alternating order in which these parts were in-

Table 3

Results of *Lamellaria diegoensis* (*L.d.*) feeding on *Cystodytes lobatus* (*C.l.*)

Date	Beginning wet wts. (g)			End wet wts. (g)			Difference (g)			Fecal Pellets Total	
	<i>L.d.</i>	<i>C.l.</i>	Control <i>C.l.</i>	<i>L.d.</i>	<i>C.l.</i>	Control <i>C.l.</i>	<i>L.d.</i>	<i>C.l.</i>	Control <i>C.l.</i>	# of pellets	wet wt. (g)
8/4 beg 8/6 end (2 days)	6.528	10.286	8.999	5.154	9.219	9.079	-1.374	-1.067	+0.08	266	0.147
							<i>C.l.</i> Net loss = -0.987 = -0.4935 g/day			= 133/day	= 0.074/day
8/8 beg 8/12 end (4 days)	5.17	13.65	16.044	5.145	11.696	15.532	-.025	-1.954	-0.512	366	0.188
							<i>C.l.</i> Net loss -1.442 = -0.3605 g/day			= 92/day	= 0.047/day
8/18 beg 8/21 end (3 days)	5.672	20.864	34.696	5.986	18.08	33.01	+0.314	-2.784	-1.686	521	0.250
							<i>C.l.</i> Net loss = -1.098 = -0.366 g/day			= 174/day	= 0.083/day
										\bar{x} = 128 \pm 38/day	\bar{x} = 0.065 \pm 0.017/day

gested. In Table 1 are the wet and dry weights for 10 pieces of *C. lobatus* colonies and for 15 daily fecal pellet accumulations for *L. diegoensis*. The calorimetric analysis of these dried materials is given in Table 2.

Several feeding experiments were carried out (Table 3) to determine the average amount of food eaten per day and correlate this with the number and weight of fecal pellets produced per day. Unfortunately the handling, blotting dry and weighing of *Lamellaria* had a definite negative effect. The results indicate, however, that the animal was acclimating (compare beginning and end weights for each of the feeding runs), and better results would probably have been obtained if the experiments had been continued longer. The feeding experiments appear so variable as to be unusable, but internal checks show a surprisingly close correlation. For example, the ratio of the number of fecal pellets produced per day during the feeding experiments (128) to the average number from Table 1 (152) is nearly the same as the ratio of the weight of dry feces produced per day during the feeding trials (15 mg) to the average dry wt. from Table 1 (17.9 mg). These two sets of numbers were obtained independently by direct measurements and counts. Between May 3 and August 4, 1978, the 3 months prior to the feeding trials, the animal increased in weight from 2.2 to 6.5 g, indicating a steady gain. Assuming that *Lamellaria* had maintained a constant weight during the feeding experiments, the average net weight loss of *Cystodytes* was $0.392 \pm .058$ g wet wt/day (all losses added together and divided by 9 days total feeding time). This value is equivalent to 0.036 g dry wt/day, or 0.013 g ash free dry wt/day after subtracting for the 63.3% ash content (Table 3). The result is 48.6 calories ingested per day.

The lamelliid produced an average of 0.065 g wet weight of feces per day during the feeding experiments. Multiplying this by the dry/wet wt ratio from Table 1 results in a value of 0.015 g dry feces/day, or 0.003 g ash free dry wt/day after subtracting the 78.8% ash content. This is equivalent to 17.9 calories/day lost in the feces. Thus, the net caloric intake for *Lamellaria diegoensis* was 30.7 calories/day (=48.6-17.9 cal/day). Given that the *Lamellaria* weighed 6.53 g at the start of the feeding experiments, on a per gram basis its daily intake would be 4.7 calories/g body wt/day. This value is probably low when compared to the average number of fecal pellets produced per day when the animal is undisturbed (Table 1). Using this latter value, one can compute that the average net caloric intake would be 36 calories/day when the animal is undisturbed, or 5.5 calories/g body wt/day.

To determine feeding preferences, a few of the ascidian species growing next to *Cystodytes* colonies in nature were offered to *Lamellaria diegoensis*. The mollusk was starved for 3 days, then placed with *Aplidium* sp., *Polyclinum planum* (Ritter & Forsyth, 1917) or didemnids (unid.) for 24 hours. In no case were any of these ascidians eaten. When the *Lamellaria* was then offered *Cystodytes* it immediately began to feed, even in rather bright light before its dish was covered with black plastic.

SUMMARY

Lamellaria diegoensis, a prosobranch gastropod, was collected intertidally on the compound ascidian *Cystodytes lobatus* at Pacific Grove, California. A description is given of the mollusk's external morphology and coloration in order to compare it with its prey. *Lamellaria diegoensis* closely resembles its prey in color and texture, and certain behavioral traits enhance its cryptic nature. It was maintained in the laboratory on a diet of only *C. lobatus* for 6 months; during this period its weight nearly tripled, from 2.2 to 6.5 grams. Several feeding experiments were performed, and these results together with bomb calorimeter values for the ascidian colonies and mollusk feces were used in computing a partial energy budget for *L. diegoensis*. During the feeding experiments, the animal ingested 48.6 calories/day, of which 17.9 calories/day were lost in the feces, resulting in a net caloric intake of 30.7 calories/day, or 4.7 calories/g body wt/day.

The caloric values given here are only preliminary; they are included in the hope that if this work is repeated they can be used on a comparative basis. All the lamelliids share a similar mode of existence; therefore their energy budgets should be comparable. Because their diet is so restricted, if a reliable conversion can be made between number of feces and calories ingested, a variety of feeding experiments are possible with little perturbation to the mollusk.

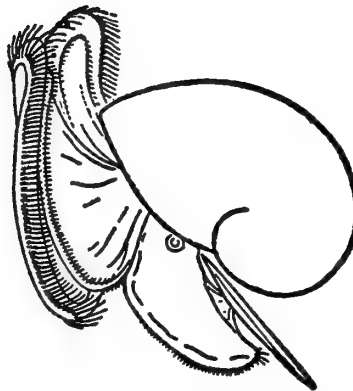
ACKNOWLEDGMENTS

I wish to thank the staff at the Hopkins Marine Station for providing space for me, in particular Dr. Donald Abbott in whose laboratory this work was carried out. Dr. Abbott's help and encouragement are greatly appreciated. David Behrens identified the *Lamellaria*, and he and Dr. Roger Seapy made valuable comments on the

manuscript. I also thank Dr. C. E. Jones and Larry Colin, who assisted me with the bomb calorimeter, and Faylla Chapman, for her willing assistance in many ways. J. Cooper, Y. Fadallah, C. Harrold, A. Hines and R. Sellers aided in subtidal collection of *Cystodytes lobatus*. I gratefully acknowledge the constant support, technical assistance and companionship of my husband Charles throughout this work.

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Stone Boring Marine Bivalves from Monterey Bay, California

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(1 Text figure)

INTRODUCTION

MONTEREY BAY HAS BEEN A CENTER for shell collecting by conchologists for more than a hundred years. Included in many of the early collections were representative bivalve borers of the families Mytilidae and Pholadidae, and Monterey Bay is the type locality for several species. SMITH & GORDON (1948) summarized these early studies and presented a list of all boring and nestling bivalves reported from Monterey Bay up to World War II. For many years after the Smith & Gordon paper appeared, little work was published on stone boring animals in Monterey Bay. In recent years, however, there has been renewed interest in this important group of animals and several theses and published papers have been partially or totally devoted to them (BOOTH, 1972; BURNETT, 1972; CLARK, 1978; DONAT, 1975; HADERLIE, 1976, 1977, 1979; HADERLIE & DONAT, 1978; HADERLIE *et al.*, 1974; MINTER, 1971).

Since 1970, a continuous long term study on marine bivalve stone borers by students and staff of the Naval Postgraduate School in Monterey has been underway. This study has consisted of two parts. First, the horizontal and bathymetric distribution and substrate preference of living borers within Monterey Bay have been investigated. This has involved extensive shore collecting, shallow water diving, and shipboard dredging operations. Second, experimental studies aimed at determining reproductive seasons, settling times, growth rates, and longevity of individual borers have been carried out. Studies have made use of experimental stone panels placed in the sea at various times and depths and for varying periods and then recovered and examined for evidence of bivalve borer settlement and growth.

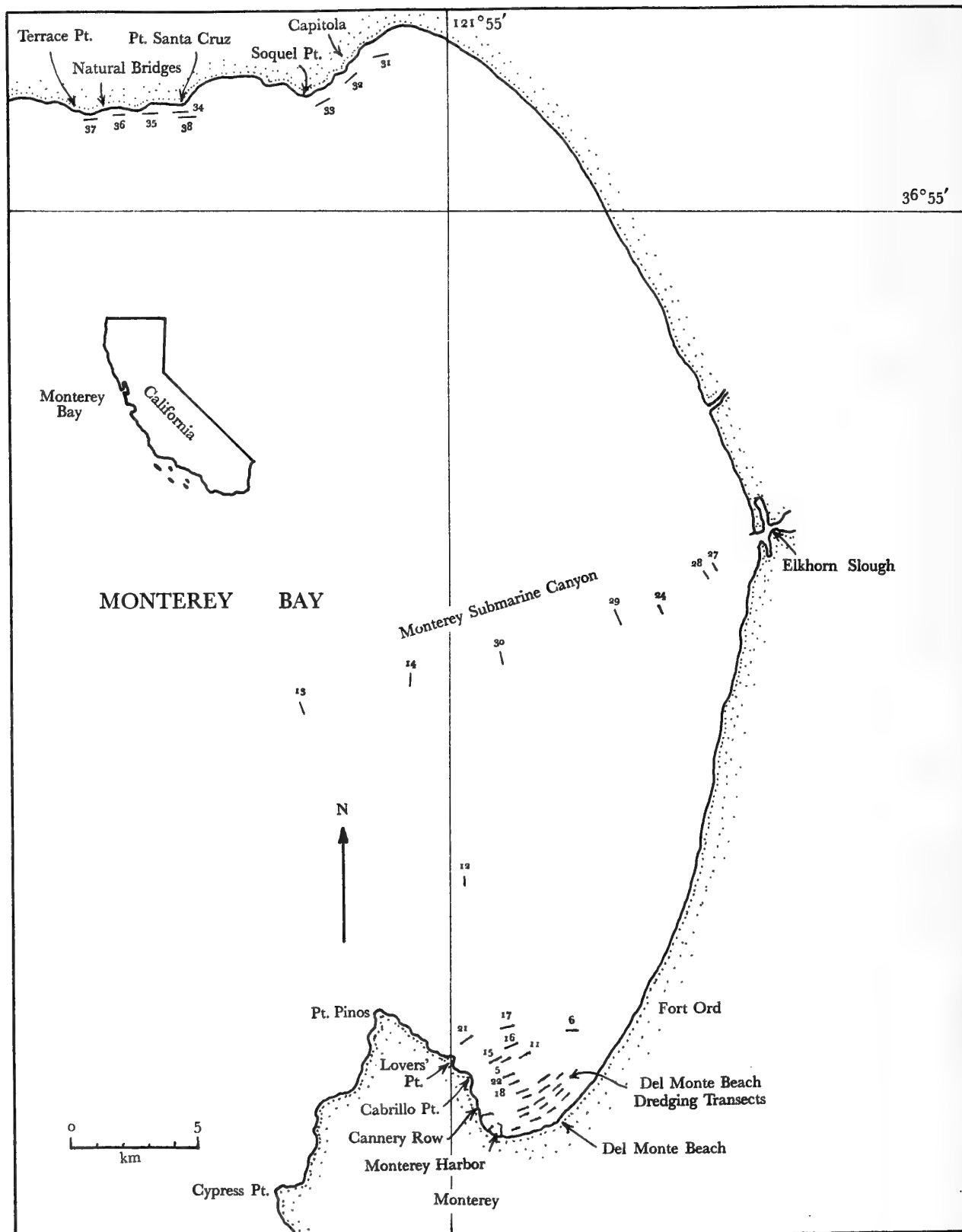
This paper presents the results to date of the first part of this study, namely the identity, distribution, abundance, and substrate preference of stone boring bivalves of the families Mytilidae and Pholadidae and associated nestlers in Monterey Bay.

ACKNOWLEDGMENTS

I want to acknowledge the help of many people, but especially Captain Reynolds and the crew of R/V *Acania* for their unfailing cooperation and help during many arduous hours of dredging operations over many years in all weather conditions on Monterey Bay. Also, I want to thank my colleagues and students who assisted in the hundreds of shallow water Scuba dives for making observations and collections, photography, or recovery of lost gear such as dredges. These include G. C. Booth, G. W. Clark, W. Donat, J. C. Mellor, C. S. Minter, and J. Norton. In the early part of the study Dr. Ruth Turner of Harvard assisted in the identification of borers and has given advice on many phases of the work. Drs. R. S. Andrews and W. C. Thompson of the Naval Postgraduate School and Dr. H. G. Greene of the U.S. Geological Survey helped in sorting out the complex geology of Monterey Bay, and Florence Lee-Wong of the U.S. Geological Survey made the petrographic analyses of thin sections of various rock samples. The office of Naval Research, Oceanic Biology Program, has provided long term financial support for this project, and the Naval Postgraduate School Research Foundation Program has assisted in the intertidal part of the project.

TOPOGRAPHY AND GEOLOGY OF MONTEREY BAY

Monterey Bay is a large open embayment along the central California coast some 115 km south of San Francisco (see Figure 1). The mouth of the Bay is about 37 km in width when measured from Point Santa Cruz in the north to Point Pinos in the south. The shoreline at the southernmost part of the Bay, on the Monterey Peninsula, is a rocky headland composed of Santa Lucia granodiorite of Cretaceous age. From Monterey eastward and north to



Soquel Point there are broad sandy beaches backed by dune fields in the south and cliffs in the north. The shoreline in the vicinity of Santa Cruz is composed of steep bluffs with flat-topped terraces. These sea cliffs are Quaternary marine terrace deposits which overlie Pliocene Purisima Formation at Point Santa Cruz. This latter formation is exposed as yellow sandstone and siltstone in the intertidal zone. To the west of Point Santa Cruz the sea cliffs are composed of Pliocene Santa Cruz mudstone overlying layers of chert of Miocene Monterey Formation. This latter formation extends as broad terraces or finger reefs interspersed with sandy pockets into the intertidal and subtidal zones.

The subtidal topography and geology of Monterey Bay is diverse and complex. The sea bottom relief is dominated by the Monterey Submarine Canyon which originates less than 2 km west of Elkhorn Slough and extends westward for over 90 km as a deep, V-shaped cut in the continental shelf. The remainder of the Bay bottom is a relatively flat, gently sloping continental shelf, covered with unconsolidated sediments and interrupted by a few rocky reef outcrops. GALLIHER (1932) was the first to publish information on the location and lithologies of these rocky outcrops. SHEPARD & EMERY (1941), MARTIN (1964), and GREENE (1977) have extended these observations in many details and have also reviewed the extensive literature on the geology of Monterey Bay. During these previous studies, and from dredge hauls made during the present investigation, rock samples from many of these outcrops and from the walls of the Monterey Submarine Canyon have been obtained. Samples of porphyritic biotite granodiorite have been dredged from off Point Pinos and from the south wall of the Monterey Canyon. This granitic rock that forms the basis of the Monterey Peninsula is apparently also the dominant basement rock under Monterey Bay. The sedimentary rocks dredged from the bottom of the Bay are mudstones, siltstones, sandstones, cherts, and conglomerates derived from the Monterey Formation of middle Miocene age and from Pliocene Purisima Formation.

AREA OF STUDY

This study has been limited to Monterey Bay which is here defined as the area to the east of a line running from Point

Pinos on the Monterey Peninsula to Terrace Point west of Santa Cruz in the north. The area of most intense study, and that from which we have the most complete data, is the shallow subtidal zone off Del Monte Beach to the east of Monterey harbor at the most southerly end of Monterey Bay (Figure 1). This area is roughly defined by the extensive kelp bed made up primarily of *Macrocystis pyrifera* (Linnaeus, 1771) whose holdfasts are attached to the discontinuous outcrops of shale of the Monterey Formation. The water depth in the area of shale outcrops is from 10 to 20 m. In most of the area the bottom consists of relatively flat smooth shale, sometimes covered with sand to varying thickness, at other times completely exposed except for low lying sand pockets. In roughly the middle of the study site off Del Monte Beach, the topography is much more rugged with hummocks and ledges distributed parallel to the trend of the Tulareitos Fracture Zone which enters the Bay from the southeast. Some of these ledges are continuous ridges rising 2 m or more above the adjacent bottom and running several hundred meters seaward. The shale in this area has been examined and sampled repeatedly over the past 10 years by Scuba diving, and the benthic fauna and flora, including the distribution of several species of boring bivalves, have been investigated (BOOTH, 1972; BURNETT, 1972; HADERLIE, 1976; HADERLIE *et al.*, 1974; MINTER, 1971).

The present investigation has continued these studies and extended them seaward by using shipboard dredging techniques to sample the exposed shale in deeper water off Del Monte Beach and throughout Monterey Bay. Some dredge hauls were made in areas previously studied by shallow water diving in order to recover larger samples of rock substrate than can be collected conveniently by divers. During this investigation, we have successfully collected bottom samples on 40 dredge hauls in Monterey Bay (Figure 1).

In addition to the subtidal areas of Monterey Bay described above, we have surveyed the intertidal zones for sedimentary rocks which might harbor bivalve borers. At the southern end of Monterey Bay along the shore of the Monterey Peninsula only granitic rock is exposed in the intertidal zone and no bivalve borers can penetrate this hard basement material. From Monterey harbor around the Bay to Soquel Point in the north, the shore consists of sandy beaches. But from Soquel Point westward to Terrace Point, sedimentary rocks of both the Purisima Formation and the Monterey Formation are exposed in the intertidal zone as reefs or sea cliffs. We selected two of these reefs to the west of Point Santa Cruz for intensive study of bivalve borers.

(← on facing page)

Figure 1

Map of Monterey Bay Area

In column Substrate Sample: Concr. = Concretions
In columns Relative Abundance, Vacant Bore Holes; and
Relative Abundance, Living Borers:
A = abundant F = few O = none

Table 1
Dredging Hauls, Samples Recovered, and Borers and Nestlers Collected

Dredge Haul No.	Date	Depth & Location	Substrate Sample	Sample Volume (cm ³)	Relative abundance,		Borers							Nesters						
					vacant bore holes	Relative abundance, living borers	<i>Adula californiensis</i>	<i>Adula falcata</i>	<i>Lithophaga plumula</i>	<i>Chaceia ovoidea</i>	<i>Nelastoma rostrata</i>	<i>Parapholas californica</i>	<i>Pentella conradi</i>	<i>Pentella gabbi</i>	<i>Pentella penta</i>	<i>Pentella fitchi</i>	<i>Crepidula perforans</i>	<i>Hiatella arctica</i>	<i>Irus lamellifer</i>	<i>Kellia laperosusii</i>
1	21 Mar 1974	22 m, off Del Monte Beach	Chert block	125,000	F	A	2	10	1	10	14						3			4
2	19 Mar 1975	24 m, off Del Monte Beach	Chert block	64,800	F	A	5	60	2	1	2	43	46	4			20	11	7	22
3	19 Sep 1975	11 m, off Del Monte Beach	Chert	1,200	F	A		2		10	2	11	1			11			1	4
4	20 Oct 1975	13 m, off Del Monte Beach	Chert	6,000	F	A				5	1	3					1			
5	18 Nov 1975	52 m, off Cabrillo Point	Chert; Concr.	1,400	A	F	2													
6	18 Nov 1975	56 m, off Fort Ord	Chert blocks	9,500	A	O														
7	18 Nov 1975	22 m, off Del Monte Beach	Chert blocks	1,800	A	A				1		1	8							
8	3 Jan 1976	11 m, off Del Monte Beach	Chert	5,400	F	A	1	3	1	2	20	45	4			4	5	3	3	3
9	18 May 1976	15 m, off Del Monte Beach	Concretions	82,500	A	A		310	1	1	4	2	4			5		1	2	4
10	10 Nov 1976	12 m, off Del Monte Beach	Chert; Concr.	9,800	F	A		87			2	1	3			2			3	6
11	6 Dec 1976	50 m, off Cannery Row	Chert; Concr.	6,500	F	A		29		1	2	4	3			1		1		3
12	7 Jan 1977	90 m, off Point Pinos	Chert	500	O	O														
13	7 Jan 1977	150 m, Monterey Canyon	Gray Mud	—																
14	7 Jan 1977	140 m, Monterey Canyon	Concretions	600		O														
15	7 Jan 1977	52 m, off Cabrillo Point	Chert; Concr.	9,300	A	A														
16	9 Feb 1977	54 m, off Cabrillo Point	Chert block	6,400	A	O									5					
17	9 Feb 1977	60 m, off Cabrillo Point	Chert; Concr.	4,200	A	F														
18	10 Mar 1977	30 m, off Cannery Row	Chert	700	F	O														
19	26 Apr 1977	15 m, off Dell Monte Beach	Chert; Concr.	12,300	F	A		30			18	10	1					2		
20	26 Apr 1977	25 m, off Del Monte Beach	Chert; Concr.	10,800	F	A		2			5	7				7			5	
21	21 Jun 1977	55 m, off Lovers' Point	Chert	8,400	A	F						2								
22	4 Aug 1977	40 m, off Cannery Row	Concretions	14,800	F	A		19			8	2	2	1		5		1	3	
23	8 Aug 1977	24 m, off Del Monte Beach	Chert; Concr.	7,500	A	A		13	1	1	7	3	1							
24	11 Aug 1977	120 m, Monterey Canyon	Gravel; Mud	—																
25	27 Sep 1977	20 m, off Del Monte Beach	Chert; Concr.	2,900	F	A		1	8	3	12	17				12	1	5	6	
26	28 Sep 1977	20 m, off Del Monte Beach	Concretion	250,000	A	A		2	28	3	2	24	25	22				10	6	
27	1 Feb 1978	90 m, Monterey Canyon	Dark Mud	—																
28	1 Feb 1978	130 m, Monterey Canyon	Dark Mud	—																
29	1 Feb 1978	160 m, Monterey Canyon	Dark Mud	—																
30	3 Feb 1978	300 m, Monterey Canyon	Purisima	600	O	O														
31	16 Feb 1978	7 m, off Capitola	Purisima	2,200	A	A	2	20	18					45		2	63	3		
32	16 Feb 1978	10 m, off Capitola	Purisima	900	A	O														
33	16 Feb 1978	7 m, off Soquel Point	Purisima	4,300	A	A	2	3	2	9	2	26	4			1	8	7		
34	16 Feb 1978	7 m, off Point Santa Cruz	Purisima	3,100	A	A	1	17	6					2		1		2		
35	23 Feb 1978	7 m, off Point Santa Cruz	Mudstone	600	F	F						4	2							
36	23 Feb 1978	7 m, off Natural Bridges	Mudstone	800	F	F														
37	23 Feb 1978	8 m, off Terrace Point	Mudstone	700	F	A	3			1	4	7				2	12	1	2	
38	20 Mar 1978	13 m, off Point Santa Cruz	Purisima	2,000	F	A	1	17	6							1	1	8	3	
39	17 Jan 1979	15 m, off Del Monte Beach	Chert	2,200	F	A														
40	1 Mar 1979	20 m, off Del Monte Beach	Chert	1,000	F	F				2		3	6			2		5		5

Monterey shale off Del Monte Beach, (2) dredging operations, (3) intertidal work near Santa Cruz, and (4) carbonate and petrographic analyses of representative rock samples.

1. DIVING OBSERVATIONS ON MONTEREY SHALE OFF DEL MONTE BEACH

The paper by HADERLIE *et al.* (1974) included a review of all diving operations and observations made in the kelp bed off Del Monte Beach up to that time. Since then, additional diving work has been done to sample parts of the exposed shale bottom that had not been examined previously. Methods and techniques employed were the same as in the earlier studies.

The following species of bivalve borers have been found while diving on the shale outcrops of the Monterey Formation off Del Monte Beach: *Adula californiensis* (Philippi, 1847), *A. falcata* (Gould, 1851), *Lithophaga plumula* Hanley, 1843, *Barnea subtruncata* Sowerby, 1846, *Chaceia ovoidea* (Gould, 1851), *Netastoma rostrata* (Valenciennes, 1846), *Parapholas californica* (Conrad, 1837), *Penitella conradi* Valenciennes, 1846, *P. gabbii* (Tryon, 1863), *P. penita* (Conrad, 1837) and *Zirfaea pilsbryi* Lowe, 1931. In addition the following molluscan nestlers have been found in vacant pholad holes: *Crepidula perforans* (Valenciennes, 1846), *Hiatella arctica* (Linnaeus, 1767), *Irus lamellifer* (Conrad, 1837), *Kellia laperousii* (Deshayes, 1839), and *Petricola carditoides* (Conrad, 1837). As will be pointed out below in the section on results from dredging, one additional species of pholad, *Penitella fitchi* Turner, 1955, was found in shale in slightly deeper water off Del Monte Beach.

Some of the borers listed above can readily be identified *in situ* by a diver, provided the animals are fairly large and the siphons are extended and exposed. These include *Barnea subtruncata*, *Chaceia ovoidea*, *Parapholas californica*, and *Zirfaea pilsbryi*. The siphons of all others are so small that, although they can be seen clearly projecting from a bored rock sample kept in an aquarium, they are exceedingly difficult to detect in the field under average diving conditions. The siphon tips of members of the genus *Penitella* can usually be distinguished from all other genera, but species determination in the field usually is impossible. Likewise, although the siphons of the mytilids *Adula californiensis*, *A. falcata*, and *Lithophaga plumula* are distinguishable from those of pholads, they are not sufficiently distinctive from species to species to allow for identification in the field.

Identification and attempts to quantify densities of populations of borers by observing the borers in place, while

diving, is further hampered by shifting sand at the Del Monte Beach diving site. Along this beach there is considerable onshore-offshore sand movement with seasons. Following the first storm waves striking the beach in November and December each year much of the sand is combed off the beach and distributed in subtidal waters out to about 10 m depth. Sand covers much of the flat shale outcrops, sometimes up to 30 cm or more in thickness, for several months of the year. Yet, as will be pointed out later, some of the bivalve borers in the shale survive this seasonal burial. Others that cannot tolerate periodic burial are limited in distribution to the projecting ledges and ridges that remain sand-free throughout the year.

As part of this over-all study, BOOTH (1972) attempted to determine the distribution and density of boring bivalves that could be identified *in situ* along two transects running seaward for 500 m off Del Monte Beach. He found a discontinuous distribution of species along each transect, and considerable variation between the transects. Booth noted that *Parapholas* and *Zirfaea* were best able to tolerate periodic sediment cover and that *Chaceia* was most commonly found boring horizontally into shale ledges. Additional diving operations since 1972 have confirmed these observations. Booth was unable to detect *Adula*, *Barnea*, *Lithophaga*, or *Penitella* species in the deeper water along the transects he studied and concluded these borers were restricted to shallow water. In other areas off Del Monte Beach, we have not only made observations while diving, but have recovered shale samples by excavating the substrate and have found representatives of all these genera except *Barnea* out to far beyond the ends of Booth's transects. Booth also concluded that variations in hardness and carbonate content of the exposed Monterey shale were the major factors influencing the inhomogeneous distribution of bivalve borers along his transects. However, recent dredging operations on the Del Monte Beach shale outcrops have allowed us to recover large blocks of Monterey Formation, particularly hard chert, and in this dense homogeneous rock we have found representatives of most of the genera of bivalve borers living side by side.

2. DREDGING OPERATIONS

Table 1 summarizes the results of the dredging operations carried out over a 5 year period from March, 1974, to March, 1979. The 40 dredge hauls listed in Table 1 are those where a sample of the bottom was recovered successfully. Many more hauls, over 60 in fact, were made where the dredge came up empty. The general location of each haul is given in Table 1 and Figure 1.

In the majority of the successful dredge hauls, sedimentary rock was recovered, but on most of the hauls made on the south wall of the Monterey Submarine Canyon only mud, clay, or gravel came up in the dredge. We made many other attempts to dredge rock from the canyon walls but collected no sample at all. This was a disappointment, for one of our objectives in this study was to sample the rocky wall of the canyon to determine if living stone borers were present and if they played a role in causing erosion and deepening of the canyon. In southern California, WARME, SCANLAND & MARSHALL (1971) found that *Parapholas californica*, *Netastoma rostrata*, *Adula californiensis*, and *Lithophaga plumula* bored intensely into the rocks of the rim and upper walls of the Scripps Submarine Canyon, and that in some areas these organisms were more important as eroders of rock than physical and chemical processes. Even though the walls of the Monterey Submarine Canyon are steep, it is apparent from our results that a sticky layer of clay covers most areas. GREENE (1977) succeeded in recovering rock samples from both the north and south walls of the Monterey Canyon. In some cases these were granite samples, in others siltstone or sandstone. Many of the non-granitic rocks Greene recovered showed bore holes made by pholads and possibly mytilids, but no living borers were found. We must tentatively conclude, therefore, that living marine bivalve borers are not causing extensive erosion of the walls of the Monterey Canyon at the present time.

In the shallow subtidal water off Santa Cruz relatively few dredge hauls were successful in recovering samples. Off Capitola and Soquel Point a few successful hauls recovered samples from the Purisima Formation, and off the terraces to the west of Point Santa Cruz some samples of chert and mudstone were recovered. Most of these samples showed evidence of stone borer activity.

In the shallow water at the southern end of Monterey Bay, we were much more successful in recovering rock samples and living bivalve borers as is indicated in Table 1. In some cases the chain bag dredge would come up with one large block of chert that had been broken off a ledge, or a large flat concretion broken out of a cherty matrix. In other cases it picked up loose pieces of chert or rounded calcareous concretions that had been lying free on the bottom. Most samples collected off Del Monte Beach consisted of a mixture of these two rock types, and most samples showed extensive borer activity leading to considerable erosion of the rock.

We have collected two species of borer bivalves from subtidal shale off Del Monte Beach while diving, yet have

never recovered either of them in dredged samples. *Zirfaea pilsbryi* is a larger pholad commonly found boring into stiff clay or hard mud at Elkhorn Slough. Off Del Monte Beach, it is relatively abundant, occupying vertical burrows in the softer shale and mudstone. The distinctive siphons made identification easy. This species is often found in densities of 5 animals per m². *Zirfaea* excavate burrows up to 60 cm deep in the shale that forms the flat bottom between elevated reefs. Dredging is therefore unlikely to recover rock samples containing *Zirfaea*. Diving observations have indicated that large animals of this species can project their siphons up through as much as 30 cm of sand cover.

A second species not collected by dredging, *Barnea subtruncata*, is somewhat smaller than *Zirfaea*. It too has distinctive siphons and lives in soft flat shale off Del Monte Beach but in numbers far fewer than *Zirfaea*.

Most of the boring bivalves found during this investigation had been collected earlier in Monterey Bay, and the subtidal shale off Del Monte Beach is the type locality for several species. One pholad, however, had never been collected before north of southern California (HADERLIE, 1979). *Penitella fitchi* was described from specimens collected from intertidal rock at Bahía San Bartolomé, Baja California (TURNER, 1955). Additional specimens have been found at Redondo Beach, La Jolla, and San Diego. Kennedy (1974) reported *P. fitchi* as a fossil in Pleistocene deposits from southern California and Baja California. During the present study, *P. fitchi* was found on four occasions. Single living animals were recovered on each of the dredge hauls numbers 20, 22 and 23. The animals were from 5.0 to 6.5 cm in shell length, were in the post-boring stage, and occupied burrows in hard chert. On Dredge Haul No. 25, a single set of valves (4.0 cm long) of a dead specimen was found in a burrow in chert.

One of the objectives of the dredging part of this study was to determine the bathymetric distribution of boring bivalves in Monterey Bay. As will be pointed out below, some species occur in the intertidal zone at Santa Cruz as high as 2 m above MLLW (mean lower low water or zero tide level). Subtidally our dredging operations have shown (Table 1) that living bivalve borers are common down to depths of 50 m in the southern part of the Bay. Below a depth of 50 m very few living animals have been found in recovered rock samples, although many rocks brought up from these deeper waters were riddled with burrows that were identical to those made by living pholads in shallower water. Many of the bored rock samples from deeper water had been broken off by the dredge, so these samples had not been transported to deeper water.

Perhaps these bore holes were made by pholads in the past when the level of Monterey Bay was lower than at present, or when temperatures were different. The vacant holes do not appear to be geologically old, however, for they were not filled with compacted sediment and were often not even occupied by nestlers. Experiments now in progress (to be reported on later) have shown that very few boring bivalve larvae settle on or bore into experimental rock panels exposed in water depths exceeding 70 m in Monterey Bay.

3. INTERTIDAL REEFS NEAR SANTA CRUZ

One of the earliest reports on living bivalve borers in the intertidal zone at Santa Cruz was in the original edition of RICKETTS & CALVIN (1939). Ricketts had observed *Platyodon cancellatus* (Conrad, 1837) in enormous numbers in banks of stiff blue clay and noted their erosive influence along the shore. He also found siphons of *Parapholas californica* projecting from rocky reefs in the intertidal zone at Santa Cruz, but the exact location of the reefs was unspecified. In this investigation we have concentrated on the rocky reefs in the area to the west of Point Santa Cruz and have not observed large numbers of living *Platyodon* nor *Parapholas*. The few living *Platyodon cancellatus* observed appeared to be nestlers in vacated pholad burrows. In the blocks of Purisima Formation in the cliffs some 5 m above sea level at Santa Cruz, however, there are many Pliocene fossils of *P. cancellatus* to be seen as was reported by ADDICOTT (1966).

Most of the results of the investigation being reported on here from the intertidal zone at Santa Cruz were included in a thesis by CLARK (1978). This past year, studies have continued, particularly on the terraces west of Natural Bridges State Park.

On one large intertidal reef composed primarily of Monterey shale west of Point Santa Cruz, Clark found the following species of bivalve borers: *Adula californiensis*, *A. falcata*, *Lithophaga plumula*, *Netastoma rostrata*, *Penitella gabbii*, *P. penita*, and *Parapholas californica*. Of these, *Penitella penita* was by far the dominant species of borer and was found in rock ranging from the hardest chert to soft mudstone, from 0.7 to 2.0 m above MLLW, and in population densities of more than 10 mature individuals per 75 cm² surface area. Most individuals were found boring horizontally into ledges on the reef, particularly in pot holes where concretions had been displaced. Approximately half the *P. penita* were in the boring stage, half were mature with a fully-formed callum. The largest individuals had a shell length (exclusive of siphonoplax) of 5.7 cm.

The mytilid *Adula californiensis* was the second most common borer found on the reef at Santa Cruz. The largest of these had a shell length of 3 cm. All the other borers were present in much smaller numbers. Nestling bivalves occupying vacant pholad holes included *Semele rupicola* Dall, 1871, *Hiatella arctica*, *Protothaca staminea* Conrad, 1837, *Petricola carditoides*, *Kellia laperousii* and *Platyodon cancellatus*.

CLARK (1978) also studied the borers in a transect across a flat, gently sloping terrace of chert and mudstone located west of Natural Bridges State Park. He found that here, too, *Penitella penita* was the dominant borer with *Adula californiensis*, *Penitella gabbii*, and *Netastoma rostrata* present in smaller numbers. The highest level where any of these occurred was at 1.0 m about MLLW where a few *Penitella penita* were found.

The broad terraces found between Natural Bridges State Park and Terrace Point are broken periodically by wide channels which cut through the terraces all the way up to the base of the sea cliff some 40 m shoreward from low water level. These channels have a floor of sand which varies in thickness throughout the year. Where these channels have cut through the terraces they have left vertical walls on each side, some 2 m or more high in some places. During this past year these exposed vertical sections of the terraces have been examined for stone borers. Shifting sand along the lower part of these walls erodes the rock very fast and many of the vertical walls are severely undercut. These regions harbor relatively few stone borers, mainly *Penitella penita* and *Netastoma rostrata*, and all individuals recovered were small and immature. It is possible that borers cannot survive long enough to reach maturity in this substrate being rapidly abraded by moving sand. In the vertical walls above the area of major sand movement, however, many *Penitella* borers were found and about half of these were large mature animals. *Penitella penita* again was the dominant species observed, but *P. gabbii* was also common. *Netastoma rostrata* and *Adula californiensis* were also present, but in small numbers. *Chaceia ovoidea* was also found boring horizontally into these intertidal rock walls. FITCH (1953) reported *Chaceia* as being common at Santa Cruz, but CLARK (1978) did not observe this species during his work on the intertidal reefs and terraces. During this past year many specimens of *C. ovoidea* have been collected from the walls of the surge channels near Terrace Point at levels of 0.5 to 1.0 m above MLLW. All of the *Chaceia* so far observed have been small, up to 1.7 cm shell length, and in the immature boring stage, and no large *Chaceia* burrows have been seen, as are common in subtidal waters off Monterey. This would indicate that even the upper walls of

the surge channels through these intertidal terraces erode away and expose the *Chaceia* before these long-lived borers become mature.

4. CARBONATE AND PETROGRAPHIC ANALYSES OF ROCK SAMPLES

The literature on rock boring organisms extends back for more than 200 years. Yet, many of the problems considered in these published studies and observations remain unresolved. At times in the past it has been fashionable to divide stone borers into two large categories, those that appear to dissolve the rock by chemical means, and those that abrade the rock mechanically. Among the bivalve borers, the mytilids, such as *Lithophaga* and *Adula*, have been considered chemical borers despite the fact there is no direct evidence to support the contention. Pholads as a whole have been considered to be mechanical borers, a conclusion based primarily on the functional morphology of these animals and their shells. The investigation being reported on here from Monterey Bay does not answer any of the lingering questions regarding the specific method or methods used by bivalves in burrowing into solid rock substrates. These studies have shown, however, that methods used for boring may be far more complex than we have suspected, and any one borer may be able to use a variety of methods for excavating burrows into various rocks having different physical and chemical properties. The fact that *Lithophaga plumula* (usually considered to be a chemical borer living primarily in calcium carbonate substrates) and various species of the genus *Penitella* (usually considered to be mechanical borers living primarily in soft rock) can live side by side and reach maximum size while boring into exceedingly hard, dense, siliceous chert in the shallow subtidal and intertidal zone of Monterey Bay indicates that we have much to learn about the fundamental mechanisms of rock boring in marine animals.

The dominant rock types where living bivalve borers have been found in the present investigation in Monterey Bay fall into three main categories: (1) silty biogenic cherts and siliceous shales of the Monterey Formation, (2) calcareous concretions of various shapes and sizes associated with the chert beds or derived from them and lying free on the bottom, and (3) Purisima Formation dredged from shallow water at the north end of the Bay. We have attempted to learn something about the physical and chemical nature of the first two types of these rocks into which many species of bivalves so regularly erode sizable burrows.

The amount of CaCO_3 in any of the samples from the Monterey Formation (except for concretions), be they relatively soft mudstone or exceedingly hard chert, was extremely low, varying from 0.03 percent in some samples to a maximum of 0.74 percent in others. Analysis of thin sections of chert from the Santa Cruz reef and from subtidal outcrops off Del Monte Beach showed it to be primarily (90 - 95%) a ground mass of siliceous biogenic hash (radiolaria, sponge spicules, diatoms, etc.) with 5-8 percent clasts of silt-sized quartz, feldspar, biotite, magnetite, hematite, and microcrystalline chert. No cementation was present.

Chemical analysis of the concretions, both from the subtidal waters in Monterey Bay and from the reefs in the intertidal zone at Santa Cruz, gave a CaCO_3 content of 80-85 percent. Thin sections demonstrated that the concretions were recrystallized fossiliferous limestone with a ground mass of muddy carbonate now recrystallized to sparry calcite. The fossils were recrystallized foraminifera and siliceous tests replaced by calcite.

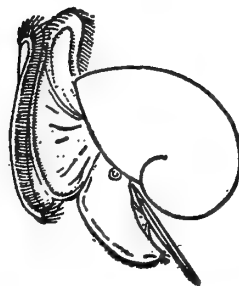
SUMMARY

1. This paper presents the results of a 10 year study on the distribution of bivalve mollusks that bore into rocky substrates in Monterey Bay.
2. Living borers were found in all types of sedimentary rocks from 2 m above MLLW to depths of over 50 m.
3. The Monterey shale exposed under the kelp beds in southern Monterey Bay has been examined by divers and 11 species of bivalve borers have been identified including the mytilids *Adula falcata*, *A. californiensis*, *Lithophaga plumula*, and the pholads *Barnea subtruncata*, *Chaceia ovoidea*, *Netastoma rostrata*, *Parapholas californica*, *Penitella conradi*, *P. gabbii*, *P. penita*, and *Zirfaea pilsbryi*.
4. Over 100 dredge hauls were made at various places in Monterey Bay from the shallow water off Santa Cruz to deep water in the Monterey Canyon. Forty of these hauls were successful in recovering a bottom sample. In water down to 50 m deep in the southern part of the Bay, rock samples recovered carried the same borers as were found in the diving operations, with the exceptions of *Adula californiensis*, *Barnea subtruncata*, and *Zirfaea pilsbryi*. In addition, the dredging recovered a species not previously reported from Monterey Bay, *Penitella fitchi*. Dredging in shallow water off Santa Cruz recovered samples of Purisima Formation with a variety of borers.

5. In deeper water of Monterey Bay, recovered rock samples showed evidence of bivalve borer activity, but no living borers were found.
6. Few samples of sedimentary rock were recovered from the walls of the Monterey Canyon and none carried living borers.
7. The intertidal reefs at Santa Cruz were populated, from low tide level to 2 m above MLLW, with *Adula californiensis*, *A. falcata*, *Lithophaga plumula*, *Chaceia ovoidea*, *Netastoma rostrata*, *Parapholas californica*, *Penitella gabbi* and *P. penita*. Of these, *Penitella penita* was the dominant species.
8. Chemical and petrographic analyses of various rock samples indicated that most of the bivalve borers in Monterey Bay bore into both siliceous rocks of various hardness and into calcareous rocks.

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Generic Variation in Sympatric Sibling Species of *Littorina*

BY

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INTRODUCTION

A NUMBER OF STUDIES on marine invertebrates have correlated spatial heterogeneity in allele frequencies at certain enzyme gene loci with the dispersal ability of organisms (WIUM-ANDERSEN, 1970; SCHOPF & GOOCH, 1971; GOOCH *et al.*, 1972; SNYDER & GOOCH, 1973; BERGER, 1973, 1977; GAINES *et al.*, 1974; WILKINS *et al.*, 1978). In general, these studies have indicated that the difference in allele frequencies between geographically separated populations is greater in species which lack a planktonic stage in the life cycle than in those with planktonic eggs or larvae, or both. Site-specific, or region-specific, alleles are also more common in the former than in the latter. These conclusions have, to a large extent, been drawn from studies on littorinids or from comparisons of other taxonomically unrelated species with littorinids. At the loci encoding esterases (BERGER, 1973) phosphoglucose isomerase and phosphoglucomutase (WILKINS *et al.*, 1978) intersite allele frequency variations are greater and site specific alleles more common in *Littorina saxatilis* (Olivi, 1792) which is ovoviviparous than in *L. littorea* (Linnaeus, 1758) which has planktonic eggs and larvae. *Littorina obtusata* (= *L. littoralis*) which has benthic eggs is intermediate between these two.

Results such as these on littorinids may be influenced by the taxonomic status of the species investigated. If, for example, *Littorina saxatilis* were composed of two or more distinct species with characteristic allele frequencies, the observed geographic variation might reflect differing distributions or proportions of these species at the various sites. The most recent evidence (HELLER, 1975) indicates that in the European area at least, "*L. saxatilis*" may comprise four separate, non-interbreeding species viz. *L. rudis* (Maton, 1797), *L. nigrolineata* Gray, 1839, *L. neglecta* Bean and *L. patula* Jeffreys. Likewise, two distinct species comprise the "*L. obtusata* (= *littoralis*)" complex viz. *L. obtusata* (Linnaeus) and *L. mariae* Sacchi & Rast. (SACCHI & RASTELLI, 1967).

We have examined over 3 000 winkles, separated morphologically into these species, from 9 sites in Ireland and

one site in France. We present here the results of the analysis of genic variability at the phosphoglucose isomerase and phosphoglucomutase loci in these samples. The results indicate that genic variability does correlate with dispersal capability for the species *Littorina rudis*, *L. obtusata* and *L. littorea*, but extrapolation from these to other species is not warranted. The significantly greater degree of genic variability in *L. rudis* is unexpected when the potential for inbreeding in this ovoviviparous species is considered.

MATERIALS AND METHODS

Samples were collected from rocky shores at 6 sites (Silverstrand, Barna, Spiddal, Carna, Doolin, Aranmore island) in or near Galway Bay on the west coast of Ireland, and from one site near each of the localities Cork (south coast), Carnsore (southeast coast), Dublin (east coast) and Brest (west coast of Brittany, France), as indicated in Table 1.

Table 1

Numbers of individuals of the six species of winkles analyzed from the various sites. SIL., Silverstrand; BAR, Barna; SPI, Spideal; CAR, Carna; ARA, Aran Island; DOO, Doolin; COR, Cork; CAN, Carnsore; DUB, Dublin; BRE, Brest.

Site	<i>Littorina littorea</i>	<i>Littorina nigro.</i>	<i>Littorina neglecta</i>	<i>Littorina rudis</i>	<i>Littorina obtusata</i>	<i>Littorina mariae</i>
SIL.	56	77	90	60	72	101
BAR.	90	118	66	127	157	79
SPI.	146	—	—	—	171	—
CAR.	60	—	54	—	77	—
ARA.	45	—	—	—	86	—
DOO.	55	52	—	75	—	—
COR.	58	61	—	25	96	—
CAN.	73	—	71	79	83	—
DUB.	90	—	—	60	160	—
BRE.	75	—	—	74	78	—
TOTALS	748	308	281	500	980	180

Not all individuals from each site were analyzed for both enzymes; the figures in Table 1 are the maximum number analyzed at one or other gene locus from each site. Species were identified and separated using the criteria described by HELLER (1975) for the *Littorina saxatilis* complex and those of SACCHI & RASTELLI (1967) for the *L. obtusata* complex. We were unable to identify winkles of the *L. patula* type in any of the samples. Individuals were maintained alive in sea-water aquaria until analyzed by the usual electrophoretic technique (WILKINS, 1977).

Allele frequencies in the different populations or species, or both, were compared by χ^2 analysis of $2 \times j$ tables of observed allele numbers, with one or two degrees of freedom as appropriate.

RESULTS

The electrophoretic patterns observed were consistent with those previously reported (WILKINS *et al.*, 1978). Phosphoglucose isomerase (Pgi) patterns indicated a dimeric enzyme encoded at a single locus in all the species, with 2, 3 or 4 alleles expressed in each species. Mobilities of the

F, F', S, and S' isozymes were similar in all species except for *Littorina littorea* in which all Pgi isozymes migrated more anodally than in the other species. Phosphoglucose patterns indicated that this enzyme is monomeric, encoded at a single locus with 1, 2 or 3 alleles in each species. Isozyme mobilities were similar in all species except *L. littorea* in which all isozymes migrated more slowly than in the other species.

Table 2 summarizes the results obtained for all 6 species at both loci. The 3 species of the *saxatilis* complex did, indeed, have characteristic allele frequency distributions: at both loci all 3 species differed significantly ($P < 0.001$), except for *Littorina rudis* and *L. neglecta* at the Pgi locus. These differences between the species were statistically significant ($P < 0.001$) at all localities where the species occurred together; *i. e.*, sympatric populations of the various species were significantly different from each other. Considering all localities, *Littorina nigrolineata* differed significantly from *L. rudis* and from *L. neglecta* at both loci in all possible between-site and inter-species comparisons. The difference between *L. rudis* and *L. neglecta* was statistically significant in all between-site comparisons at the Pgm locus, but only in 2 of 24 comparisons at the Pgi locus.

Table 2

Summary of genic variability at the Pgi and Pgm loci in six species of *Littorina*.

Species	Phosphoglucose Isomerase						Phosphoglucose mutase				
	N _p	N _t	pF	pS	pF'	pS'	N _p	N _t	pF	pF'	pF'
<i>Littorina littorea</i>	10	747	0.957 (0.0070)	0.043 (0.0070)	—	—	10	593	0.951 (0.0051)	0.021 (0.0028)	0.028 (0.0070)
Saxatilis complex											
<i>Littorina nigrolineata</i>	4	308	0.955 (0.0125)	0.045 (0.0120)	—	—	4	299	0.840 (0.0560)	0.141 (0.0595)	0.026 (0.0145)
<i>Littorina neglecta</i>	4	281	0.682 (0.0225)	0.280 (0.0080)	0.048 (0.0170)	—	3	216	0.412 (0.1062)	0.541 (0.0895)	0.048 (0.0173)
<i>Littorina rudis</i>	6	416	0.708 (0.0245)	0.257 (0.0253)	0.026 (0.0061)	0.015 (0.0012)	7	473	0.539 (0.0227)	0.322 (0.0442)	0.015 (0.0299)
Obtusata complex											
<i>Littorina obtusata</i>	8	891	.714 (0.0159)	0.235 (0.0134)	0.050 (0.0088)	—	8	691	0.327 (0.0251)	0.673 (0.0255)	0.006 (0.0)
<i>Littorina mariae</i>	2	180	0.585 (0.0092)	0.412 (0.0057)	0.006 (0.0071)	—	2	180	1.00	—	—

N_p = number of populations sampled.

N_t = number of individuals analyzed.

pF, pF', pS, pS' = mean frequencies of the various alleles. The number in parentheses under each allele frequency is the standard error of the mean frequency (S.E.M.).

Littorina obtusata differed significantly from *L. mariae* at both loci. This difference between them was statistically significant ($P < 0.001$) at each of the localities (Silverstrand and Barna) from which both species were collected, and the differences were also significant in all comparisons of the 2 species considered over all sites.

Interpopulation variation in allele frequency was less in *Littorina littorea* than in most of the other species. This is reflected in the generally lower standard error of the mean given with each allele frequency in Table 2. Interspecific comparisons of allele frequency variance are more meaningful when restricted to sites common to all the species sampled. Thus, when *L. littorea*, *L. obtusata* and *L. rudis* representing species which have planktonic eggs, benthic eggs and internally brooded eggs, respectively, were compared over the 5 sites from which samples of all 3 species

populations of *Littorina littorea* were compared in all possible pairwise combinations, no statistically significant differences in allele frequency were observed in any comparison at either locus. In contrast, *L. obtusata* populations differed significantly in 8 out of 28 comparisons (29%) at the Pgi locus and in 14 out of 28 comparisons (50%) at the Pgm locus. *Littorina rudis* populations differed significantly in 2 out of 15 comparisons (13%) at the Pgi locus and in 18 out of 21 comparisons (86%) at the Pgm locus.

In Table 4 the observed heterozygosity is compared between the various species and their mode of reproduction is indicated. Heterozygosity levels are significantly lower in *L. littorea* and *L. nigrolineata* than in any of the other species, excepting *L. mariae* where a single allele is fixed at the Pgm locus.

Table 3

Comparison of allele frequencies at the Pgi and Pgm loci in *Littorina littorea*, *Littorina obtusata* and *Littorina rudis* from the six sites at which all three species were collected. Site abbreviations as in Table 1.

Site	Phosphoglucose isomerase						Phosphoglucomutase					
	<i>L. littorea</i>		<i>L. obtusata</i>		<i>L. rudis</i>		<i>L. littorea</i>		<i>L. obtusata</i>		<i>L. rudis</i>	
	F	S	F	S	F	S	F	S	F	S	F	S
SIL.	0.938	0.063	0.721	0.214	0.746	0.246	0.955	0.027	0.375	0.625	0.667	0.208
BAR.	0.967	0.033	0.732	0.194	0.702	0.250	0.972	0.011	0.349	0.651	0.406	0.370
COR.	0.931	0.069	0.690	0.288	0.740	0.220	0.956	0.018	0.432	0.568	0.391	0.457
WEX.	0.979	0.021	—	—	0.684	0.289	0.918	0.014	0.325	0.675	0.481	0.430
DUB.	0.944	0.056	0.728	0.241	0.600	0.358	0.938	0.025	0.228	0.772	0.707	0.195
BRE.	0.947	0.053	0.615	0.288	0.777	0.203	0.954	0.033	0.218	0.776	0.561	0.365
MEAN	0.951	0.049	0.697	0.245	0.708	0.261	0.949	0.021	0.321	0.679	0.536	0.338
S.E.M.	0.007	0.008	0.022	0.019	0.026	0.023	0.008	0.003	0.034	0.034	0.054	0.045

were collected (Table 3), the standard error of the mean frequencies increased from *L. littorea* through *L. obtusata* to *L. rudis*. Although the lower variability in *L. littorea* may be attributable to the more extreme values of the allele frequencies in the species (variance decreases as allele frequency approached 1 or 0), the variance of *L. obtusata* was consistently less than that of *L. rudis*, but their mean frequencies were of intermediate value and similar to each other.

At the population level, these differences in geographic variability between the species were most obvious. When

DISCUSSION

The absence of significant gene exchange between *Littorina rudis* and *L. nigrolineata* which is indicated by their different allele frequencies at all localities, but especially at those (Silverstrand, Barna, Doolin and Cork) where sympatric populations were studied, strongly supports the proposal of HELLER (1975) that these constitute 2 separate biological species. *Littorina nigrolineata* is also clearly different at both loci, even in sympatric populations, from

Table 4

Mode of reproduction and degree of genetic variability in winkles.

Species	Reproduction			Phosphoglucose isomerase				Phosphoglucomutase			
	Mode	Egg	Larva	N _t	N _a	Het	p	N _t	N _a	Het	p
<i>Littorina littorea</i>	ovip.	planktonic	planktonic	747	2	0.078	0.957	593	3	0.099	0.951
<i>Littorina nigrolineata</i>	ovip.	benthic	non-planktonic ¹	308	2	0.090	0.955	299	3	0.118	0.840
<i>Littorina obtusata</i>	ovip.	benthic	crawling	891	3	0.447	0.714	691	3	0.472	0.673
<i>Littorina mariae</i>	ovip.	benthic	crawling	180	3	0.508	0.585	180	1	0.00	1.00
<i>Littorina rudis</i>	ovovivip.	brooded	crawling	416	4	0.395	0.708	473	3	0.582	0.539
<i>Littorina neglecta</i>	ovovivip.	brooded	crawling	281	3	0.413	0.682	216	3	0.495	0.541

¹Oviparity, with benthic eggs, was described for forms now classified (Heller, 1975) as *L. nigrolineata* as early as 1947, in a much neglected report by Seshappa (1947). Heller (1975) indicates that the larvae are non-planktonic but we are not aware of any published record of this fact. Indeed, the resemblance of *L. nigrolineata* to *L. littorea* in its reduced heterozygosity would be easily explained if *L. nigrolineata* proves to have planktonic larvae.

N_t = number of individuals analyzed.

N_a = number of alleles detected.

Het = proportion of heterozygotes observed.

p = mean frequency of the commonest allele.

L. neglecta. However, it has been reported that copulation by male *L. rudis* with individuals other than conspecific females may be as high as 50%, and male *L. nigrolineata* exhibit similar non-selectivity in copulatory behavior (RAFFAELLI, 1978). For each species, "wrong" copulations comprise those made with conspecific males and with males and females of the other species. The difference observed here between the allele frequencies in sympatric populations of these species indicate that those "wrong" copulations which involve females are not reproductively successful. On this genetic evidence, together with morphological and other data (HELLER, 1975; SACCHI *et al.*, 1977), *L. nigrolineata* can be regarded as a good species reproductively isolated from both *L. rudis* and *L. neglecta*.

Littorina rudis and *L. neglecta* differ only at the Pgm locus. Since this difference is statistically significant ($P < 0.001$) over all localities, and especially in sympatric populations (Silverstrand, Barna, Carnsore), it indicates that uninterrupted gene flow does not occur between these species either. *Littorina obtusata* and *L. mariae* differ at both loci in sympatric populations and these genetic data support the other evidence (SACCHI & RASTELLI, 1966; GOODWIN & FISH, 1977) used to distinguish these species. The absence of hybridization between *L. littorea* and any of the other species is unequivocal since *L. littorea* shared no allele at either locus with any of the other species and no individual was observed to possess a combination of any

L. littorea allele with one from another species. In view of the widespread citation of these littorinid species, especially "*L. saxatilis*," in studies on the ecology, physiology and behavior of littoral organisms, a detailed survey of the distribution of the various species is warranted, particularly on the east coast of North America where the presence of *L. nigrolineata* Gray, *L. neglecta* Bean and *L. mariae* Sacchi & Rastelli, 1966 has yet to be determined.

The observations made here on geographic variability and its correlation with dispersal capability confirm the earlier results of BERGER (1973) and WILKINS *et al.* (1978) for the species *Littorina rudis*, *L. obtusata* and *L. littorea*. In neither of these earlier papers were the species within the *saxatilis* and *obtusata* (*littoralis*) complexes precisely identified. While supporting the earlier results for these species, the extended data presented here indicate that the correlation of genic variability with dispersal capability is not simple, and extrapolation from these to other, even other littorinid, species is not justified. Compare, for example, the Pgm allele variances of oviparous *L. nigrolineata* and ovoviparous *L. rudis*, or the Pgi allele variances of oviparous *L. obtusata* and ovoviparous *L. neglecta* (Table 2).

We wish to draw attention to one final interesting feature of the data: this is the high absolute level of genic heterozygosity in the ovoviparous species (*Littorina rudis* and *L. neglecta*, Table 4). This observation is not

confined to the two loci studied here. High overall heterozygosity was also observed by BERGER (1978) at other loci in *L. saxatilis* (precise species not indicated, but probably *L. rudis*) from Roscoff and from Cape Cod. In all studies involving littorinids, the ovoviviparous *L. saxatilis* has consistently exhibited significant levels of genic heterozygosity, especially when contrasted with *L. littorea*. In ovoviviparous littorinids the fertilized ova are retained within the brood pouch of the female until development is complete, when a crawling juvenile emerges. There is no active dispersal phase in the life cycle and the juveniles live largely within the range of their own parents. Under such circumstances, effective population sizes are small and inbreeding is likely to be common. Since inbreeding and random genetic drift in populations of small effective size both act to increase homozygosity, the observed high heterozygosity is most unexpected. The possibility cannot be excluded that individuals of a newly recognised species, *Littorina arcana* (HANNAFORD ELLIS, 1978) may have been included among those identified here as *L. rudis*. *Littorina arcana* resembles *L. rudis* in shell and penial characters, but differs in reproducing oviparously (HANNAFORD ELLIS, *op. cit.*). If our *L. rudis* samples are indeed a mixture of these two species (although we have no reason to suspect they are), this could explain the high genic variability observed. This possibility needs further investigation. However, no such problem exists in the case of *L. neglecta*: in this ovoviviparous species at least, natural selection must favour heterozygotes strongly in order to maintain the actual levels of heterozygosity observed.

SUMMARY

Sympatric populations of the sibling species *Littorina rudis* (Maton), *L. neglecta* Bean and *L. nigrolineata* Gray, all until recently regarded as subspecies or varieties of *L. saxatilis* Olivi, have different allele frequencies at the gene loci encoding phosphoglucose isomerase and phosphoglucose mutase. Sympatric populations of *L. obtusata* (Linnaeus) and *L. mariae* Sacchi & Rastelli also differ significantly from each other at these loci. Geographic variability at these loci is greatest in *L. rudis* and least in *L. littorea*, but the correlation of genic variability with dispersal capability is less obvious than previously reported. The unexpectedly high absolute level of heterozygosity in ovoviviparous *L. rudis* and *L. neglecta* indicates that natural selection maintains variability in these species.

ACKNOWLEDGMENTS

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Range Extension and Notes on the Feeding of the Nudibranch *Okenia cupella*

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THE DORID NUDIBRANCH *Okenia cupella* (Vogel & Schultz, 1970) was first described from specimens collected in the York River, Virginia (VOGEL & SCHULTZ, 1970). Other specimens were later found in the Chesapeake Bay (MARCUS, 1972) and Wachapreague Channel, Virginia (VOGEL, 1977). Distribution outside the Chesapeake Bay area has not previously been reported. Two specimens were found in Delaware Bay (approximately 200 km N of the mouth of Chesapeake Bay) by Daniel Deckard and myself in July 1978. These and additional specimens were found associated with and feeding on the ctenostome bryozoan *Anguinella palmata* van Beneden, 1845, which is common on subtidal portions of pilings on the Henlopen Tidal Flats, Cape Henlopen State Park, Lewes, Delaware. The nudibranchs were found in this area until the end of November, and only on *A. palmata*. The total length of adult specimens preserved in 70% ethanol, measured from mouth to the most posterior tip, ranged from 1.2 to 2.4 mm, with a mean of 1.66 mm. They appeared most common during the months of September and October when 8 to 10 individuals at a time could be found on a large zoarium.

In a preliminary laboratory prey-preference test, in 6 separate trials, 2 individuals of *Okenia cupella* consistently identified and chose *Anguinella palmata* over 3 other species common in the area: *Bugula stolonifera* Ryland, 1960, *Schizoporella unicornis* (Johnston, 1847), and *Alcyonidium polyomm* (Hassall, 1841). In this test, the

nudibranchs were placed in the center of a large glass evaporating dish (20 cm inner diameter) with zoaria of each of the 4 bryozoan species distributed at equal distances from each other along the periphery of the bowl. The dish was then placed in the dark for 45 minutes. At the end of this time the nudibranchs' positions were noted with respect to that of the prey.

To feed on the arborescent *Anguinella palmata*, an individual of *Okenia cupella* first crawls out onto a bryozoan's terminal branch, where the feeding zooids are located. The nudibranch aligns itself lengthwise along the branch, with its head near, but not on, the tip. It grasps the branch with propodium and oral lobes and begins to feed. It eats through the zooid's lateral wall, the polypide, and the opposite wall as well, consuming the terminal 1.0 to 1.5 mm of the zooid in about one hour at 22° C. The nudibranch then spends a period of time in mating, in egg laying, or in inaction before moving to another branch to repeat the feeding process.

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Two New Molluscan Species

(Gastropoda : Muricidae)

from the Tropical Eastern Pacific

BY

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(1 Plate)

RECENT DREDGING IN DEEP WATER near Guaymas, Sonora, Mexico, has yielded two previously undescribed species of the Muricidae. Both species were obtained in sufficient numbers, including living specimens, and are so distinctly different from recognized taxa, as to warrant immediate description.

Murexiella Clench & Pérez Farfante,
1945

Type Species: *Murex hidalgoi* Crosse, 1869, by OD

The small, stoutly fusiform shell possesses four or more varices with foliated spines connected by a laminated webbing. The siphonal canal is moderately broad and extended. The operculum is muricoid, with a sub-apical nucleus.

Murexiella mildredae Poorman, spec. nov.

Description: Shell small for the genus but massive in structural detail. Protoconch large, of 2½ whorls somewhat flattened on the sides, with the tip immersed, and terminating in a small varix. Teleoconch of 5 whorls. Axial sculpture begins with 8 small varices per whorl but de-

creases to 5 relatively high, rounded varices on the final adult turn. There are 3 strong spiral cords on each whorl except for the last. On that whorl, there are 6 on the body, 2 much smaller cords on the constricted region below the aperture, and 2 strong cords on the canal. All cords broadly rounded, narrower at the base than at the top, and overhanging the narrow interspaces. Cords marked by 3 or 4 incised spiral grooves and are nodose from incremental growth, especially along the edges. Each cord begins high up in the preceding hollow spine and descends sharply across the front of the varix. The cords grow stronger as they rise on the back of the next varix and terminate in blunt, hollow, recurved spines, strongest at the shoulder. Aperture nearly oval, slightly pointed posteriorly; but there is no apparent anal sulcus. Peristome completely erect, crenulated along the outer lip by the 6 spiral cords. Crenulations disappear a short distance within the aperture; there is no other dentition. Operculum muricoid, with a sub-basal nucleus. Suture constricted. Each varix extends diagonally across the shoulder like a buttress to the heavy spine, to grow small and disappear just before the suture. Each shoulder varix is marked at the crest by 3 weak spiral cords which show no trace on the smooth shoulder. The peristome of each growth stage extends across the shoulder in front of the varix and appears as an overlay on the shoulder of the next growth stage. The siphonal canal is long, narrowly open to the right, and distally recurved. Previous terminations of the canal form a diagonal line from the inner lip down the canal to the left.

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The color of the shell is pale waxen brown, shading to darker brown on the varices, and darkest on the spines. Spiral color banding (if present) is restricted to a single brown cord at the anterior end of the aperture.

Type Locality: 5 km S of Tetas de Cabra, Estero San Carlos, Sonora, Mexico; 27°54' N Lat., 111°05' W Long., 9 specimens dredged in 100 m on broken shell, small rock, and silt bottom.

Holotype: Los Angeles County Museum of Natural History no. 1913.

Dimensions of the holotype: Height 19.7 mm, maximum diameter 10.8 mm.

Paratypes: 1 paratype is at the National Museum of Natural History, Smithsonian Institution, catalogue no. USNM 749091; 1 paratype is at the San Diego Natural History Museum, catalogue no. SDNHM TS 511; 3 paratypes are in the Carl & Laura Shy Collection, Westminster, California; 3 paratypes are in the Leroy & Forrest Poorman Collection.

The new species is not similar to any other recognized *Murexiella* from the Eastern Pacific fauna. While vaguely resembling the juvenile form of *M. laurae* Vokes, 1970a, it differs from that species in the number of varices on the adult whorl, the form of the spiral cords and spines, ornamentation on the shoulder, and details of coloration.

This lovely species is named in recognition of my sister, Mildred Poorman, a master teacher for 44 years, and one who has been a major influence in my life.

Carl & Laura Shy generously contributed the holotype (LACMNH no. 1913) and one paratype (SDNHM TS 511). This is gratefully acknowledged.

Pazinotus E. H. Vokes, 1970b

Type Species: *Eupleura stimpsonii* Dall, 1889, by OD

Small shells with axial ornamentation consisting of 4 to 7 varices formed by lamellar flanges. Spiral ornamentation moderate, terminating in strong, recurved varical spines. Aperture with strong dentition inside the outer lip. Siphonal canal open and short.

tation moderate, terminating in strong, recurved varical spines. Aperture with strong dentition inside the outer lip. Siphonal canal open and short.

Pazinotus advenus Poorman, spec. nov.

Description: Protoconch of 2 convex whorls followed by the teleoconch of 5 whorls. Suture constricted. There are 2 spiral cords on the spire and 4 on the body whorl. Cords are low and broad, stronger on the trailing edge of the varix and terminating in prominent, broadly open, recurved spines. The spine at the shoulder is the largest and is flexed toward the apex. Axial sculpture of 7 thin lamellae beginning at the suture and extending nearly to the end of the siphonal canal. Leading edge of the varix, especially within the hollow bases of the spines, frilled by several thin undulating layers of shell material. Entire surface spirally striated. The shell material is soft and much eroded on the spines and the apex. Aperture sub-oval, slightly pointed posteriorly. Operculum muricoid, with a basal nucleus. Outer lip flared, undulated at each strong cord, and slightly erect. Five strong denticles on a ridge of callus slightly below and within the outer lip. Lip adherent above, erect over the columella, and terminates as a flange with a deep chink between it and the fasciole. Canal short, open, recurved to the right, and distally reflected. Shell color light tawny brown with a darker brown band at the base of the body whorl and a second discontinuous band on the shoulder.

Type Locality: 5 km S of Tetas de Cabra, Estero San Carlos, Sonora, Mexico; 27°54' N Lat., 111°05' W Long.; 7 specimens dredged in 100 m on broken shell, small rock, and silt bottom.

Holotype: Los Angeles County Museum of Natural History no. 1914.

Dimensions of the holotype: Height 18.3 mm, maximum diameter 10.3 mm.

Explanation of Figures 1 to 4

Figures 1 and 2: Holotype of *Murexiella mildredae* Poorman, spec. nov.

Figures 3 and 4: Holotype of *Pazinotus advenus* Poorman, spec. nov.



Figure 1



Figure 2



Figure 3

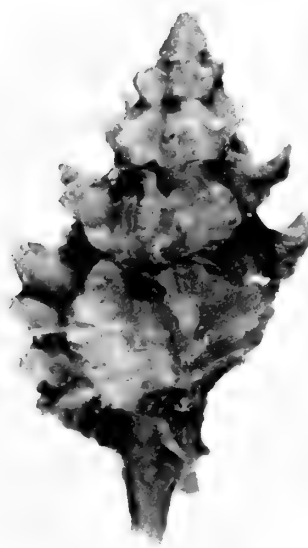


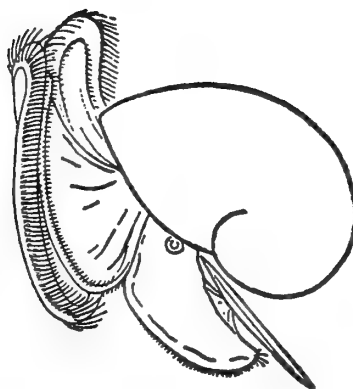
Figure 4

Paratypes: 1 paratype is at the National Museum of Natural History, Smithsonian Institution, catalogue no. USNM 749092; 2 paratypes are in the Carl & Laura Shy Collection; 3 paratypes are in the Leroy & Forrest Poorman Collection.

This new species appears to be the Eastern Pacific analog of *Pazinotus stimpsonii* (Dall, 1889), whose type locality is "off the Barbados in 120-200 meters." *Pazinotus advenus* differs in having one less spiral cord and in the darker coloration. This is the first representative of the genus in the Panamic Province.

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On the Taxonomic Position, the Species and the Paleoecological Significance of the Genera

Eubora, *Toxosoma* and *Littoridina* (?)

in the Pliocene Pebas Formation of the Upper Amazon Region

(Gastropoda : Prosobranchia)

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(17 Text figures)

INTRODUCTION

THE TERTIARY SEDIMENTS of the Upper Amazon Basin, known as Pebas Formation (also named Iquitos Formation, *e.g.*, RUTSCH, 1952), contain a peculiar molluscan fauna which has been studied by GABB (1868), CONRAD (1871, 1874), H. WOODWARD (1871), BOETTGER (1878), ETHERIDGE (1879), DE GREVE (1938) and others. However, not all of the Mollusca have been studied satisfactorily. In this study it will be shown that the generic and even family position of some gastropods described from that formation has been incorrectly recognized; the taxonomic changes will affect interpretation of the ecological importance of the species concerned. Further, it will be pointed to the possibility of a biostratigraphical subdivision of the Pebas Formation based on different evolutionary levels of the species assemblages.

Formerly, the Pebas Formation was supposed to be of Oligocene age (*e.g.*, BOETTGER, 1878). More recently (*e.g.*, RUTSCH, 1952), it is placed into the Pliocene. An indication to this age is the occurrence of the Bivalve genus *Pachydon* Gabb, 1868, frequent in the Pebas Formation, in brackish water strata of Venezuela not older than Upper Miocene (with *Ammonia beccarii* (Linnaeus)).

The depositional environment has for a long time been considered to be brackish water because of the occurrence of the genus *Pachydon* which belongs to the marine bi-

valve family Corbulidae, and because of the occurrence of species of the families Neritidae, Hydrobiidae and Dreissenidae (inhabiting fresh and brackish waters), Lacunidae (marine to brackish waters) and Assimineidae (marine, supralittoral), while typical fresh water assemblages (with Planorbidae and Ampullariidae) were missing or rare. Therefore, a connection to the sea had been postulated which Rutsch supposed to have existed across Venezuela to the Caribbean (a distance of 3000 km). However, it will be shown that the species referred to Hydrobia, Assiminea and to the family Lacunidae probably do not belong to groups of marine or brackish water inhabiting animals, thus weakening the arguments supporting the brackish water character of the whole faunal assemblage.

MATERIAL

THE ENTIRE MATERIAL EXAMINED has already been published by different authors. It is preserved in the following institutions:

BM(NH): British Museum (Natural History), Department of Paleontology, London (WOODWARD, 1871 and ETHERIDGE, 1879).

NYSM: New York State Museum and Science Service, Albany, N.Y. (CONRAD, 1871).

- PIMUZ: Palaeontologisches Institut und Museum der Universität Zürich (DE GREVE, 1938).
 SMF: Natur-Museum Senckenberg, Frankfurt/M. (BOETTGER, 1878).
 UPP: Université de Paris, Collection de Paléontologie (COSSMANN, 1915).

ACKNOWLEDGMENTS

I wish to express my sincerest thanks to the responsible persons of these institutions who enabled the loan of the material or the examination of the collections: R. Conrad (NYSM), J. Cooper (BM(NH)), K. A. Hünemann (PIMUZ), C. P. Nuttall (BM(NH)), D. Pajaud (UPP), A. Zilch (SMF).

PROVENANCE OF THE EXAMINED MATERIAL

The descriptions of the fossiliferous localities and the way that the fossils have taken from these localities may be compiled here (identical numbers refer to the same locality):

CONRAD, 1871:

Species: *Ebora crassilabra* Conrad, 1871 and *Ebora bella* Conrad, 1871 (now genus *Eubora* nom. nov.); Hauxwell collected, material sent to Conrad via Orton.

Localities: 1) Pebas, near the mouth of the Ambiyacu River, few shells; 2) South side of the Marañon River near Pichua, W of Cochaquinas, 48 km below Pebas; laminated and colored clays, "nearly the whole collection."

WOODWARD, 1871:

Species: *Ebora crassilabra* Conrad, 1871 (= *Eubora crassilabra* and *E. woodwardi* n. sp.), *Eubora bella* (Conrad, 1871) (not published by Woodward, but present in his collection); Hauxwell collected the material and sent it to Janson (London).

Localities: 1) near Pebas, Orton collected (?); 2) South side of the Marañon near Cochaquinas.

CONRAD, 1874:

Species: *Ebora crassilabra* Conrad, 1871 (now *Eubora*, nom. nov.), *Toxosoma eboreum* Conrad, 1874 and *Lio-*

soma curta Conrad, 1874 (both conspecific); Steere collected and sent the material to Eug. W. Hilgard.

Localities: 3) "near Tabatinga," blue clay with seams of dirty coal; 1) Pebas, 1.6 km off the mouth of the Ambyacú River, 18-21 m above the water level. Section: 8' clay, red and white, and sand (= soil and alluvial formations); 20' blue clay, with 4' of fossiliferous beds; 6" coal seam; 15' blue clay, with 3' of fossiliferous beds; 4) Old Pebas, ca. 3.2 km below the mouth of the Ambyacú River, at the water level; 5) Pichana, ca. 24 km away from the mouth of the Ambyacú River.

BOETTGER, 1878:

Species: *Lacuna (Ebora) crassilabris* (Conrad) Boettger, 1878 (= *Eubora crassilabra* Conrad, 1871), *L. (E.) bella* (Conrad, 1871), *L. (E.) bella semisculpta* Boettger, 1878 (both = *Eubora bella* s. str.), *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874). Juan Hauxwell collected the material, which Boettger received via P. Abendroth and W. Kobelt.

Localities: the same as of Conrad, 1871 and Woodward, 1871.

C. B. BROWN, 1879, and ETHERIDGE, 1879:

Species: *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874), *Assimineia crassa* Etheridge, 1879 and *Hydrobia dubia* Etheridge, 1879 (both = *Littoridina? crassa*).

Locality: Brazil, "cliff of the Javary River, at Canama, 200 yards above the little settlement of that name, and some 50 miles up, in a straight line, from the mouth of the Javary." Clay, bluish and greenish-blue, in part with calcareous concretions, lignite seam.

COSSMANN, 1915 figured and described material sent to him by Boettger.

GREVE, L. DE, 1938:

Species: *Lacuna (Ebora) crassilabris* (not of Conrad, 1871, comprises *Eubora woodwardi* n. sp., *E. grevei* n. sp., *E. pygmaea* n. sp.), *Pseudolacuna macroptera* Boettger, 1878 (= *Toxosoma eboreum* Conrad, 1874).

Locality: Cliff of the Itaya River near the telegraph station of Iquitos.

TAXONOMIC TREATMENT

Legend for the synonymy list of the species:

v: the original material was examined (at least partly).

*: a new name of the species name group is validly published with this reference.

?: doubtful synonymy.

Eubora Kadolsky, new name

Type species, *Ebora crassilabra* Conrad, 1871

1871 *Ebora* CONRAD, p. 194 (type by monotypy: *Ebora* (*Ebora*) *crassilabra* Conrad, 1871) (not *Ebora* Walker, 1867, p. 415).

1871 *Ebora* (*Nesis*) CONRAD, p. 194 (type by monotypy: *Ebora* (*Nesis*) *bella* Conrad, 1871 (not *Nesis* MULSANT, 1850: 67, not STÅL, 1860: 67)

Diagnosis: Shell medium-sized, ovate-conical; two embryonic whorls with deep sutures and fine growth lines; the first one coiled nearly in a plane; the next very slowly, the succeeding more rapidly descending; later whorls about 4, regularly increasing, sutures only moderately deepened; surface sculptured with growth lines, very fine incised spiral lines and in some forms with strong spiral keels. Growth lines and outer lip opisthocyrt in its adapical portion, abapically of the periphery protruded and prosocline, thus forming an inverted "S". Outer lip often reflected and thickened; aperture isometric, angular at the junction of parietal and palatal margins, and at the junction of columellar and parietal margins and truncated abapically by a siphonal (?) notch. Umbilicus closed, but a pseudumbilicus may be formed by the strongly thickened and elevated columellar margin. This pseudumbilicus is surrounded by an umbilical ridge which ends in the siphonal (?) notch. Umbilical ridge, pseudumbilicus and siphonal (?) notch not present in juveniles.

Former work on the relationships of the genus: CONRAD (1871; 1874) did not indicate an opinion on the taxonomic position of the genus. WOODWARD (1871) and BOETTGER (1878) assumed a relationship with the genus *Lacuna* Turton, 1827; Boettger even considered *Ebora* Conrad to be a subgenus of *Lacuna*. This view has been maintained in principle up to today, with the alteration that *Ebora* Conrad, 1871 was synonymized with *Pseudocirsope* Boettger, 1907 and suppressed because of its homonymy with *Ebora* Walker, 1867. So did COSSMANN (1915) and WENZ (1939). Because of the assumed synonymy with *Pseudocirsope*, no substitute name was proposed for the preoccu-

pied *Ebora* Conrad. Contrary to these authors, PILSBRY (1944) maintained *Ebora* as a distinct genus and indicated a relationship to *Potamolithus* Pilsbry, 1911, family Amnicolidae.

The type species of *Ebora* Conrad is sculptured with growth lines only, while *E. bella* Conrad exhibits several strong spiral keels. Upon this character, Conrad founded the subgenus *Nesis* which is preoccupied as well as is *Ebora* Conrad. BOETTGER (1878) and probably WENZ (1939) did not consider the presence of spiral keels to be of subgeneric importance, but WOODWARD (1871) did so. COSSMANN (1915) placed *Eubora bella* even into the genus *Fossarus* Philippi which has only very remote relationships to *Lacuna* (*Pseudocirsope*) where Cossmann placed *E. crassilabra*. The spiral keels are here considered to be of minor taxonomic significance, as they display a high interspecific variability (compare *Eubora woodwardi*, *E. grevei* and *E. crassilabra*).

Discussion of possible relationships of the genus *Eubora*

a) *Cirsope* (*Pseudocirsope*) O. Boettger, 1907

The attribution of *Eubora* to *Pseudocirsope* is now considered to be erroneous as based on convergence in shell characters. Distinguishing features are:

1) The growth lines of *Pseudocirsope* are straight, slightly prosocline to orthocline, and are not protruded abapically, while those of *Eubora* are opisthocyrt in its adapical portion, grading into prosocline ones in its abapical portion.

2) *Pseudocirsope* has a true though small umbilicus while *Eubora* has only a pseudumbilicus formed by the elevation of the thickened columellar margin in adults.

3) *Pseudocirsope* has in general a small funicle while *Eubora* has none.

4) *Pseudocirsope* has in general conspicuous spiral striae while *Eubora* has extremely delicate spiral lines only and in some cases spiral keels.

5) Umbilical ridge and siphonal notch are present in *Pseudocirsope* throughout ontogeny, while in *Eubora* they make their appearance in late ontogenetic stages and increase in strength with increasing age.

The homocomorphic features are the general shape of the shell and of the aperture and the presence of an umbilical ridge and of a siphonal (?) notch. However, as the shape of the growth lines is a tool to distinguish higher

taxonomic categories (families, superfamilies), the growth lines indicate that *Eubora* and *Pseudocirsope* must belong to different families or even superfamilies.

As pointed out by KADOLSKY (1973), the growth lines in the families Littorinidae and Lacunidae of the superfamily Littorinacea are invariably prosocline to orthocline. In that paper, the taxon *Pseudocirsope* has been removed from the genus *Lacuna* and subgenerically attributed to the genus *Cirsope* Cossmann, 1888 (s.l.), which in a restricted sense formerly has been treated as a subgenus of *Lacuna* as well as *Pseudocirsope*. The relationship between *Cirsope* and *Lacuna* appears not to be very close, and in future *Cirsope* may be classified anywhere in the Prosobranchia Mesogastropoda. Any classification differing from that in the family Lacunidae, however, would not affect the above statement that *Eubora* and *Pseudocirsope* are homoeomorphs.

b) Genera from the Pebas Formation

Tropidebora Pilsbry, 1944: This genus is almost certainly related to *Eubora*, as it differs mainly in possessing a strong peripheral keel and a blunt shoulder on the adapical portion of the whorls. It has a siphonal (?) notch, a pseudumbilicus, a ridge contouring the umbilical area and a thick parietal callus, which are also characteristic of *Eubora*.

Toxosoma Conrad, 1874: Differs mainly by the presence of a supracolumellar fold and also by a more protruded outer lip in adult specimens. By all other characters a close relationship to *Eubora* is proven.

c) *Potamolithus* Pilsbry, 1911

The type species, *P. rushi* Pilsbry, 1911, has no apertural notch although there is a ridge surrounding the umbilical area. As in the juvenile stage the columella is "semicircular," while it is narrow in *Eubora*, this feature may be homoeomorphous. However, many other species placed by PILSBRY (1911) in *Potamolithus* have an apertural notch and also a pseudumbilicus. These species may in fact be related to *Eubora*; at present the nominal genera are separated as the type species of *Potamolithus* lacks essential characters of *Eubora*, and it cannot be completely ruled out that PILSBRY (*op. cit.*) assembled a heterogeneous community under the heading of *Potamolithus*, or that features in common are homoeomorphous. For example, species of both genera may have spiral keels, but their pattern differs: *Eubora* may have 7 keels which may become reduced to 3 or to nil, while *Potamolithus* species may have 1-3 strong keels.

d) *Lithococcus* Pilsbry, 1911

Although superficially similar to keeled *Eubora* species by its sculpture, *Lithococcus* lacks an apertural notch and is therefore unrelated to *Eubora*.

e) *Mexithauma* Taylor, 1966

As in *Lithococcus*, *Mexithauma* resembles *Eubora* by the presence of spiral keels. However, *Mexithauma* has strictly prosocline growth lines, no apertural notch, a much less developed pseudumbilicus (only in largest specimens) and no umbilical ridge.

Eubora crassilabra (Conrad, 1871)

(Figures 3-4, cf. Figure 5)

v*1874 *Ebora* (*Ebora*) *crassilabra* Conrad, p. 194; pl. 10, fig. 14; two localities mentioned: nearly the whole collection was obtained from "nearly 30 miles below Pebas, on the south side of the Marañon, at Pichua, just west of Cochaquinas"; minor collections "at Pebas, near the mouth of the Ambiyacu."

Holotype: NYSM 9194, 9.0 : 6.5 mm, here Figure 3, probably from the first-mentioned locality; no paratypes preserved.

v 1871 *Ebora crassilabra* - Woodward, p. 102 (near Cochaquinas and near Pebas) (partly; fig. is *Eubora woodwardi* n. sp.)

? 1874 *Ebora crassilabra* - Conrad, p. 32, pl. 1, fig. 9 (no locality given; figure may be *Eubora woodwardi* n. sp.)

v*1878 *Lacuna* (*Ebora*) *crassilabris* - Boettger, p. 494, pl. 19, figs. 1a-d ("Pebas," same provenance as the type material).

1915 *Lacuna* (*Pseudocirsope*) *crassilabris* - Cossmann, p. 102.

1944 *Ebora crassilabris* - Pilsbry, p. 150.

Diagnosis: Shell elongate ovate-conical; sculptured with growth lines and very delicate spiral lines only. Umbilical ridge and siphonal notch distinct. Outer and inner lip markedly thickened; inner lips raised over the body whorl, columellar lip forming a pseudumbilicus; outer lip expanded.

Relations: Most closely allied is *Eubora woodwardi*, n. sp., which differs from *E. crassilabra* in being somewhat smaller, relatively broader ovate-conical (for measurements see Figures 1, 2) and with weaker umbilical ridge, weaker siphonal (?) notch and lesser thickened lips.—*Eubora pygmaea* n. sp. has half the size of *E. crassilabra*, but is in its shape and apertural characters very similar;

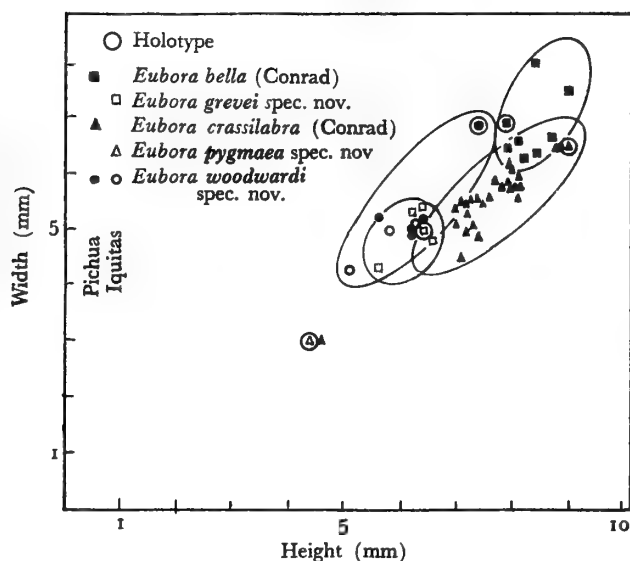


Figure 1

Crossplot height:width of the available material of the species of *Eubora* Kadolsky, nom. nov.

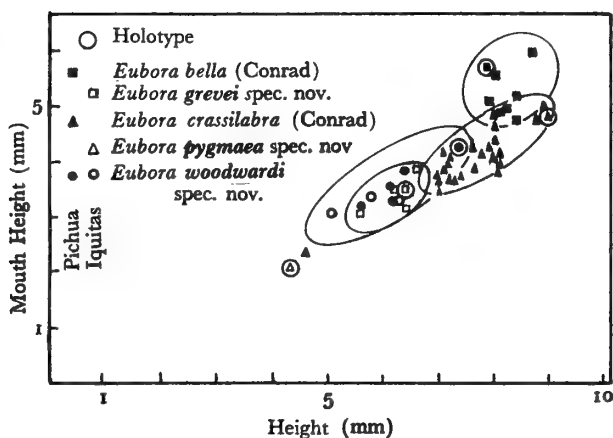


Figure 2

Crossplot shell height:mouth height of the available material of *Eubora* Kadolsky, nom. nov.

juvenile specimens of *E. crassilabra* (cf. Figure 5) differ in being completely devoid of umbilical ridge, siphonal (?) notch and pseudumbilicus.—*Eubora bella* (Conrad) and *E. grevei*, n. sp. are broader in shape and provided with spiral keels.

Nomenclatorial Remarks: Two closely related species occur at Cochaquinas which hitherto have been confused: *Eubora crassilabra* (Conrad) and *E. woodwardi*, n. sp. Unfortunately, the original figure of *E. crassilabra* is inadequate, while the figure of Woodward published in the same year (1871) is excellent but represents the latter-named species. The holotype of Conrad's species, however, restricts the meaning of the species name to the larger, more conical and more slender form, which furthermore is much more frequent at the type locality.—*Lacuna crassilabris* Boettger, 1878 is an unjustified emendation of the specific name.

Material and localities: Probably all material from Pichua near Cochaquinas (NYSM 9194, holotype; BM(NH) GG 19830/1-25, Woodward, 1871; SMF XII. 2918a, 1 spec., Boettger, 1878).

Eubora woodwardi Kadolsky, spec. nov.

(Figures 6-8)

v 1871 *Eubora crassilabra* – Woodward, p. 102 (part), plt. 5, figs. 1a, b (near Cochaquinas and near Pebas) (not Conrad, 1871).

v 1938 *Lacuna (Eubora) crassilabris* – DE GREVE, p. 70-72 (part), plt. 5, fig. 22 (Iquitos) (not *crassilabris* Boettger, 1878; not figs. 19, 20, 21, 23 which are *Eubora grevei* n. sp.).

Holotype: BM(NH) GG 19831/1, figured by Woodward, 1871, plt. 5, fig. 1 and this paper, Figure 6. Height, 7.4 mm; width, 6.9 mm.

Type Locality (hereby restricted): Pichua W. Cochaquinas, Upper Amazon Basin, Peru.

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by the broadly ovate-conical shape of the shell, the absence of spiral keels and the development of umbilical ridge, pseudumbilicus, siphonal notch and thickening of lips less pronounced than in the closely related *E. crassilabra*, particularly in specimens remaining smaller than *E. crassilabra*.

Relationships: Juvenile specimens of *Eubora crassilabra* cannot be distinguished from *E. woodwardi*, as apertural and siphonal properties of *E. crassilabra* as well as of *E. woodwardi* are late ontogenetic features and the shell proportions of juveniles are very similar (see crossplots height/width and height/mouth height, Figures 1, 2).—*Eubora grevei* n. sp. is very closely related, too, as its shell

shape is nearly identical. It is, however, easily distinguished by the presence of spiral keels.

Variability: For variability of the height, width and mouth height see Figures 1 and 2; the specimens of Iquitos are generally smaller than those of Pichua.

Localities and Material: Pichua W of Cochaquinas (BM(NH) GG 19831, holotype and 4 paratypes); Iquitos, Itaya River cliff near the telegraph station (PIMUZ, 3 paratypes, Figures 7 and 8 of this paper); all Pebas Formation, (?) Pliocene.

Eubora bella (Conrad, 1871)

(Figures 9-10)

- v*1871 *Ebora* (*Nesis*) *bella* CONRAD, p. 194, plt. 10, fig. 17 (localities mentioned: nearly the whole collections were obtained "nearly 30 miles below Pebas, on the south side of the Marañon, at Pichua, just west of Cochaquinas"; minor collections "at Pebas, near the mouth of the Ambiyacu." Holotype NYSM 9193, in this paper Figure 9, probably from the first-named locality. No paratypes preserved).
- v 1871 *Ebora* (*Nesis*) *bella* - WOODWARD, p. 102-103, plt. 5, fig. 3 (copy of Conrad's fig. 17).
- v 1878 *Lacuna* (*Ebora*) *bella* - BOETTGER, p. 494-495, plt. 13, fig. 3 ("Pebas," same provenance as Conrad's material).
- v*1878 *Lacuna* (*Ebora*) *bella* var. *semisculpta* Boettger, p. 495, plt. 13, fig. 2 (Holotype: SMF XII 2920a, in this paper Figure 10; probably from Pichua W. of Cochaquinas.)
- 1915 *Fossarus bellus* - COSSMANN, p. 88.
- 1938 *Lacuna* (*Ebora*) *bella* - DE GREVE, p. 72-73.

Diagnosis: A species of *Eubora* characterized by the broad ovate-conical shape, the relatively large size and the presence of 6 to 7 spiral keels of which 2 to 3 remain uncovered by the succeeding whorl.

Relationships: *Eubora grevei* n. sp. is certainly the nearest ally as it displays 3 spiral ribs which are equivalent to the 3 adapical keels of *E. bella*. However, *E. grevei* remains smaller, the apertural and siphonal (?) characters being less developed. The "variety" *semisculpta* Boettger, 1878, was founded on a single specimen with weaker spiral keels, but this specimen is no intermediate to *E. grevei* as the keels are still stronger developed than in *E. grevei* which further lacks the two umbilically positioned ones and the adapically positioned one. The latter, however, is not even present in all specimens of *E. bella*.

Variability: For variability of shell height, width and mouth height see crossplots Figures 1 and 2. The spiral keels vary in strength, the most adapically positioned one (Figure 10) is often absent.

Localities and Material: Pichua W. of Cochaquinas, Pebas Formation, Pliocene (NYSM 9193, holotype; BM(NH) GG 19832, 5 specimens, Woodward collection, although WOODWARD (1871) stated to possess no specimens; SMF XII 2919a-20a, 2 specimens, Boettger collection: *bella* s. str. and *bella semisculpta* Boettger, holotype).

Eubora grevei Kadolsky, spec. nov.

(Figure 11)

- v 1938 *Lacuna* (*Ebora*) *crassilabris* - DE GREVE, p. 70-72 (part), plt. 5, figs. 19, 20, 21, 23 (not fig. 22 which is *E. woodwardi* n. sp.) (not *Ebora crassilabra* Conrad, 1871, nor *Lacuna* (*Ebora*) *crassilabris* Boettger, 1878).

Holotype: PIMUZ J/4, Figure 11 of this paper; height, 6.4 mm; width, 5.0 mm; coll. de Greve, no. 266.

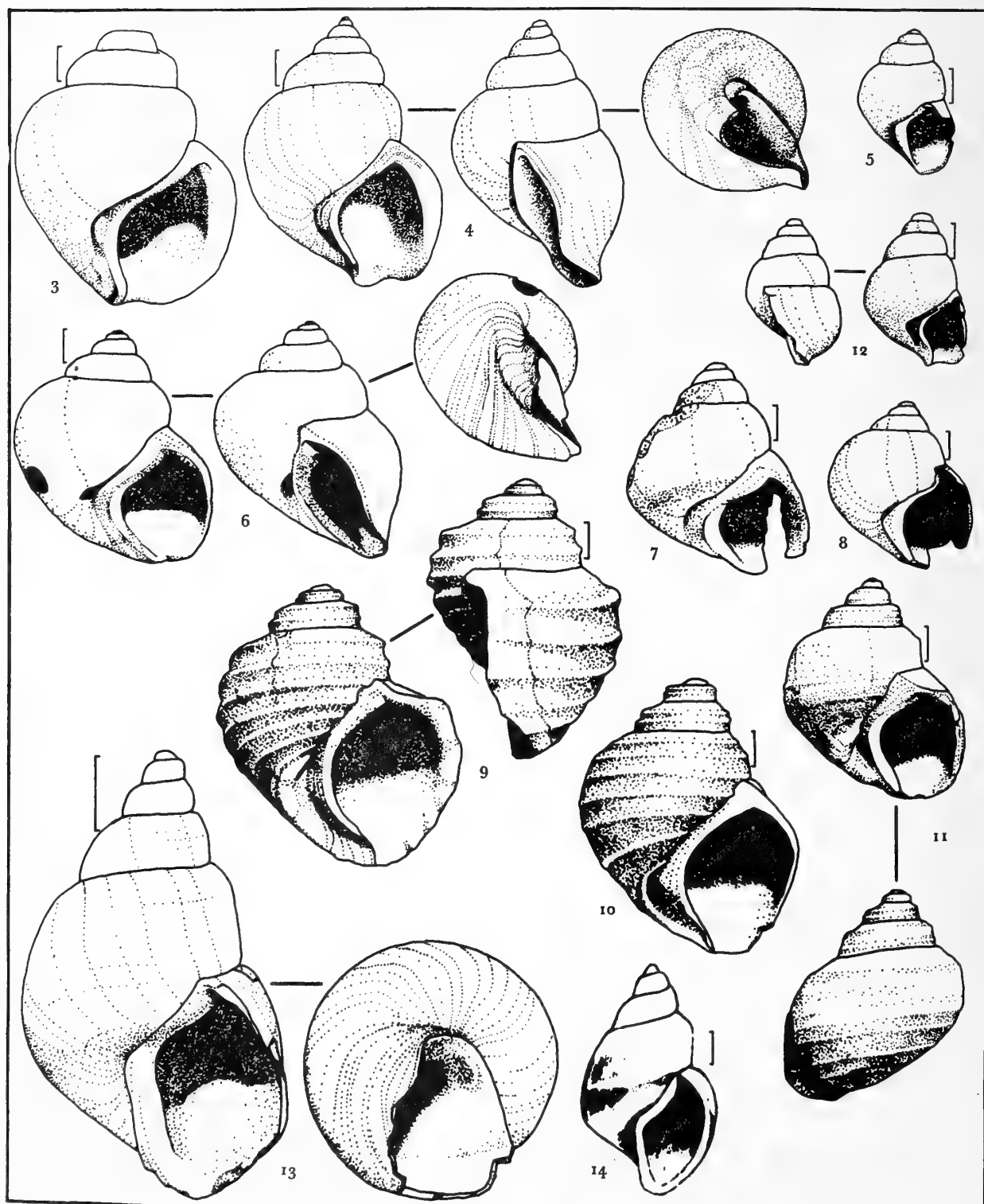
Type Locality: Peru, Upper Amazon Basin, Iquitos, Itaya river cliff near the telegraph station, locality VI of DE GREVE, 1938.

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by the broadly conical-ovate shape of the shell, the presence of three spiral ribs two of which remain uncovered by the succeeding whorls, the apertural characters and the size similar to that of *E. woodwardi*, but less developed than in *E. crassilabra*.

Relationships: The species occurs together with *E. woodwardi*, in Iquitos, and is distinguished mainly by the presence of spiral ribs. The shell of *E. grevei* seems to be somewhat more slender than that of *E. woodwardi*, but the crossplots Figures 1 and 2 show overlaps indicating that this difference derived from few specimens may not be significant.—*E. bella* has two more keels on the umbilical side and occasionally one more near the suture; all keels are much stronger developed, the size of the shell is larger and the apertural and siphonal (?) properties are stronger developed than in *E. grevei*. Doubtless *E. grevei* and *E. bella* are directly related to each other.

Localities and Material: Pebas Formation, Pliocene: Iquitos (PIMUZ, holotype and 6 paratypes, collection de Greve, nos. 263-270).



Eubora pygmaea Kadolsky, spec. nov.

(Figure 12)

v 1938 *Lacuna (Ebora) crassilabris* - DE GREVE, p. 70-72 (part, figs. excluded; not *crassilabra* Conrad, 1871, nor *crassilabris* Boettger, 1878).

Holotype: PIMUZ J/2, Figure 12 in this paper; height 4.8 mm, width 3.7 mm; collection de Greve no. 249.

Type Locality: Peru, Upper Amazon Basin, Iquitos, Itaya river cliff near the telegraph station.

(← on facing page)

Figures 3 to 14

Eubora crassilabra (Conrad, 1871)

Figure 3: Holotype, NYSM 9194, probably from the southern bank of the River Marañon at Pichua, near Cochaquinas
Figure 4: BM(NH) GG 19830/1, probably the same locality, Woodward collection

Eubora cf. *E. crassilabra* (Conrad, 1871)

Figure 5: BM(NH) GG 19836, probably the same locality as of Figs. 3 and 4; juvenile specimen, may be *E. woodwardi*

Eubora woodwardi Kadolsky, spec. nov.

Figure 6: Holotype, BM(NH) GG 19831/1. Southern bank of the River Marañon at Pichua, near Cochaquinas. WOODWARD, 1871: plt. 5, fig. 1

Figure 7: Paratype, PIMUZ J/3, Itaya River cliff near Iquitos; collection de Greve no. 262

Figure 8: Paratype, PIMUZ J/5, collection de Greve no. 268; same locality as Figure 7

Eubora bella (Conrad, 1871)

Figure 9: Holotype, NYSM 9193, probably from the southern bank of the River Marañon at Pichua, W of Cochaquinas

Figure 10: Holotype of *Lacuna (Ebora) bella semisculpta* Boettger, 1878; probably same locality, SMF XII 2920a

Eubora grevei Kadolsky, spec. nov.

Figure 11: Holotype, PIMUZ J/4, collection de Greve no. 266; Itaya River cliff near Iquitos

Eubora pygmaea Kadolsky, spec. nov.

Figure 12: Holotype, PIMUZ J/2, collection de Greve no. 249; same locality as Figure 11

Littoridina ? *crassa* (Etheridge, 1879)

Figure 13: Lectotype, BM(NH) GG 19833/1; Javary River cliff near Canama

Figure 14: Lectotype figure of *Hydrobia dubia* Etheridge, 1879: plt. 7, fig. 11; same locality as Figure 13

All fossils are from the Pebas Formation, Pliocene, of the Upper Amazon Basin. The scales represent 1 mm

Type Level: Pebas Formation, Pliocene.

Diagnosis: A species of *Eubora* characterized by its very small size (half of *E. crassilabra*), conical shape of the spire, lack of sculpture, weakly curved growth lines being prosocline rather than like an inverted "S"; apertural characters diagnostic for the genus distinctly developed.

Relationships: The new species is founded on a single specimen erroneously determined as *Eubora crassilabra* by de Greve. From this species, however, it is easily distinguished by its size, having only nearly half the height of *E. crassilabra* but having 1 more whorl than juvenile specimens of the latter (cf. Figure 5) which, moreover, are devoid of the apertural and siphonal (?) properties of the adult specimens. The growth lines are also different, being more weakly curved in *E. pygmaea*. — *Eubora woodwardi*, *E. grevei* and *E. bella* (Conrad) are much larger, too, and different in their shape, being more broadly ovate-conical. The two latter-named species have spiral ribs or keels. — *Littoridina*? *crassa* (Etheridge) is of comparably small size, but devoid of umbilical ridge, pseudumbilicus, siphonal (?) notch and elevated columellar margin, the sutures are more deepened and a weak and irregular spiral ornamentation can be seen.

Material: Only the holotype.

Littoridina? *crassa* (Etheridge, 1879)

(Figures 13 - 14)

v* 1879 *Assiminea crassa* ETHERIDGE, p. 86-87 (lectotype designated herein, fig. 13, BM(NH) GG 19833/1, Brazil, Canama, Pebas Formation).

*1879 *Hydrobia dubia* Etheridge, p. 86; plt. 7, fig. 11 (lectotype figure, here redrawn Figure 14; Brazil, Canama, Pebas Formation).

Diagnosis: A species referred with some doubt to the genus *Littoridina*, as the rhomboidal aperture and the stepped contours of the whorls are somewhat atypical for that genus. The species is characterized by its conical shape, relatively small size, deeply incised sutures and the slope of the whorls strongly rounded in the adapical portion, then only slightly convex to straight and steeply sloping, thus causing step-like contours of the spire; sculptured with growth lines and irregular spiral striae.

Relations and Generic Attribution: The species is in general characters similar to juvenile *Eubora crassilabra*, especially in missing the apertural features characteristic of the genus *Eubora* (Figure 5); the species, however, are distinguished by the shape of the spire being conical in

L.? *crassa* instead of being ovate-conical in *E. crassilabra*, the angle between columellar and parietal lip being smaller, and the whorls more evenly rounded in *E. crassilabra*.

The shells of the genus *Hydrobia* Hartmann, 1821 are more slender, the angle between columellar lip and parietal lip is much more rounded and the whorls are more evenly rounded. *Assimineae* Fleming, 1828 has a similar broadly conical shape, but the growth lines are orthocline, not curved like an inverted "S".

Synonymy and Types: The lectotype figure of "*Hydrobia dubia*" Etheridge is so similar to the lectotype of "*Assimineae*" *crassa* Etheridge that they have to be considered to be conspecific. The measurements differ little (Etheridge's figure of "*Hydrobia dubia*": height ca. 6.7 mm; lectotype of *crassa*: height 6.0 mm) but this difference is not significant. No syntypes of *Hydrobia dubia* Etheridge are present in the British Museum (Natural History). To explain this lack, one might assume that the types of *Hydrobia dubia* were confounded with those of *Assimineae crassa*. However, Etheridge stated to possess two specimens of his *Hydrobia dubia*, but the syntypic material of *Assimineae crassa* consists of three specimens. Thus, at least one specimen cannot belong to the syntypes of *Hydrobia dubia* but could be a syntype of *Assimineae crassa*. Unfortunately, Etheridge did not indicate the number of specimens of his *Assimineae crassa*. Of the three specimens of the British Museum, one was loose while two were pasted on a pasteboard. As a confusion of the syntypes cannot be proven, all three specimens are considered to be syntypes of *Assimineae crassa* Etheridge, 1879. Preference is given to the specific name *crassa* Etheridge, 1879 over *dubia* Etheridge, 1879 because of the existence of original material.

Locality and Material: Pebas Formation, Pliocene: Brazil, Canama, cliffs of the Javary river (BM(NH) GG 19833: lectotype and 2 paratypes of *Assimineae crassa* Etheridge, 1879).

Genus *Toxosoma* Conrad, 1874

- 1874 *Toxosoma* CONRAD, p. 31. Type by monotypy: *Toxosoma eboreum* Conrad, 1874.
- 1874 *Liosoma* CONRAD, p. 31. Type by monotypy: *Liosoma curta* Conrad, 1874. (Not *Liosoma* Brandt, 1835, nor Fitzinger, 1843, nor Agassiz, 1846).
- 1878 *Pseudolacuna* BOETTGER, p. 495-496. Type by monotypy: *Pseudolacuna macroptera* Boettger, 1878.

1879 *Alycaeodonta* ETHERIDGE, p. 85 (footnote) (nomen nudum, published in synonymy of *Pseudolacuna* Boettger, 1878).

Diagnosis: Shell similar to that of *Eubora*, but with a supracolumellar fold, and occasional thickenings on the columellar and parietal lips and on the palatal shell wall; outer lip thickened and strongly expanded over the preceding whorl; growth lines distinctly opisthocyrt in the apical portion and prosocyrt in the abapical portion.

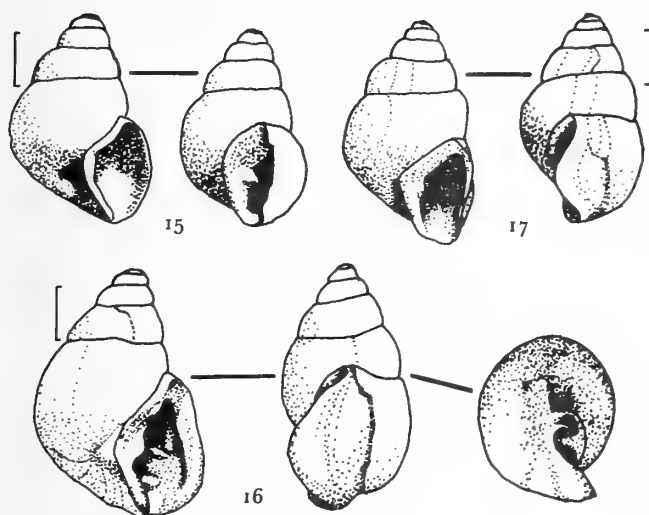
Relationships: *Toxosoma* Conrad is closely related to *Eubora*, but the above mentioned characters justify a separation on the genus level. The genus *Toxosoma* Conrad is proposed to be placed tentatively in the family Hydrobiidae s. lat. (superfamily Rissoacea) instead of family Lacunidae (superfamily Littorinacea) for the same reasons as given for the genus *Eubora*.

Toxosoma eboreum Conrad, 1874

(Figures 15-17)

- *1874 *Toxosoma eborea* CONRAD, p. 31; plt. 1, fig. 7 (localities mentioned p. 26: Tabatinga, Pebas, Old Pebas and Pichana, collected by Steere; holotype in Academy of Natural Sciences of Philadelphia, no. 161152 (see PILSBRY, 1944)).
- *1874 *Liosoma curta* CONRAD, p. 31; plt. 1, fig. 8 (for localities see *Toxosoma eboreum* Conrad).
- v*1878 *Pseudolacuna macroptera* BOETTGER, p. 496, plt. 13, figs. 14-15 ("Pebas," J. Hauxwell collected; localities according to CONRAD, 1871; Pichua W. of Cochiquinas ("nearly the whole collection") and mouth of the Ambiyacu river near Pebas (few specimens); holotype, UPP, here Figure 15; no syntypes in Boettger's collection, SMF).
- v 1879 *Pseudolacuna macroptera* - ETHERIDGE, p. 85, plt. 7, fig. 12 (Canama).
- v 1915 *Pseudolacuna macroptera* - COSSMANN, p. 107, plt. 12, figs. 27-30 (holotype, here Figure 15; sent by Boettger to Cossmann; UPP, Cossmann collection no. 15485).
- v 1938 *Pseudolacuna macroptera* - DE GREVE, p. 74-76; plt. 5, figs. 17, 18, 24-29 (Iquitos).
- v 1939 *Pseudolacuna macroptera* - WENZ, p. 514, fig. 1347 (copy Boettger, 1878).
- 1944 *Toxosoma eboreum* - PILSBRY, p. 151, fig. 3a, b (type).
- 1969 *Toxosoma eborea* - PARODIZ, p. 121.

Diagnosis: Shell small, spire irregularly conical to ovate conical, sculptured with fine growth lines only; strong



Figures 15 to 17

Toxosoma eborea Conrad, 1874

Figure 15: Holotype of *Pseudolacuna macroptera* Boettger, 1878; UPP, collection Cossmann no. 15485. Probably from the southern bank of the River Marañon at Pichua, W of Cochaquinas

Figure 16: BM(NH) GG 19834/1, collection Etheridge; Javary River cliff near Canama

Figure 17: PIMUZ J/1, collection de Greve no. 246A; Itaya River cliff near Iquitos

All fossils are from the Pebas Formation, Pliocene, of the Upper Amazon Basin. The scales represent 1 mm

supracolumellar fold invariably present; thickenings on the columella, on the parietal wall and on the palatal wall may be developed, particularly in gerontic stages; in adults parietal and columellar lip strongly thickened and elevated, causing a deep pseudumbilicus umbilical ridge becoming acute, outer lip either thickened, expanded, tending to become straight to concave in the middle portion, and ascending on the penultimate whorl (Figure 16) or only slightly expanded and strongly protruding at the periphery.

Type Material: The holotypes of *Toxosoma eboreum* Conrad, 1874 and of *Pseudolacuna macroptera* Boettger, 1878 are adult individuals with broken outer lips; *Liosoma curta* Conrad, 1874 is based on a not fully grown individual with ovoid shape and less pronounced apertural features; no original material was available.

Localities and Material: Pebas Formation, Pliocene: Brazil, Canama (BM(NH) GG 19834/1-3, Etheridge, 1879, here Figure 16); Peru, Iquitos (PIMUZ, numerous spec., de Greve, 1938; here Figure 17 (PIMUZ J/1)); Peru, probably Pichua W of Cochaquinas (BM[NH] GG 19835/1-6: "Amazon Valley, Coll. Mr. Hauxwell. Purch'd 1870"; UPP, holotype of *Pseudolacuna macroptera* Boettger 1878, here Figure 15).

Relationships of the species of *Eubora* and *Toxosoma* and their stratigraphical importance

The different localities yielded different species assemblages of *Eubora* which could be of phylogenetical and thus of stratigraphical importance. The species assemblages are:

Pichua and Pebas: *Eubora crassilabra*, *E. woodwardi*, *E. bella*, *Toxosoma eboreum*.

Iquitos: *Eubora woodwardi*, *E. grevei*, *E. pygmaea*, *Toxosoma eboreum*.

Canama: *Littoridina?* *crassa*, *Toxosoma eboreum*.

Of these faunules, that of Canama is inconclusive, showing only the species *crassa* questionably assigned to *Littoridina*, and *Toxosoma eboreum* which occurs in nearly all localities.

Eubora grevei of Iquitos is very closely allied to *E. bella* of Pichua/Pebas, differing in the weakening of the spiral keels in late ontogenetic stages and — due to the smaller size — by the less pronounced apertural and siphonal (?) characters. Also in *Eubora woodwardi*, the specimens of Iquitos are markedly smaller than those of Pichua/Pebas. Furthermore, *Eubora woodwardi* and *grevei* of Iquitos are rather closely allied (the main difference is the absence resp. presence of spiral keels), while in Pichua/Pebas *E. woodwardi* and *E. bella* (this species is directly allied with *E. grevei*) are clearly separated by their characters.

Thus, the conclusion might be drawn that the fossiliferous beds of Iquitos represent a lower stratigraphical level coinciding with the branching of the keeled and not keeled forms of *Eubora* whereas in the beds of Pichua/Pebas the keeled and not keeled forms are widely separated not only by their sculpture but by their shell dimensions and proportions too (see Figures 1, 2). Moreover, another form (*E. crassilabra*) may be interpreted to have been branched off the *E. woodwardi* stock by adding an additional whorl to the primitive form of *E. woodwardi* (of Iquitos, with small size), increasing more slowly in volume, thus contributing more to the height increase than to the width increase of the shell.

Otherwise, the phylogenetical relations could be interpreted to be inverse, i.e., the fauna of Pebas being ancestral to that of Iquitos, when regarding the early ontogenetic presence of keels in *Eubora grevei*. Assuming the keeled species of *Eubora* evolved from smooth ones, one would expect that the keels made their first appearance in late ontogenetical stages, while a property already developed may vary most strongly in late ontogenetical stages, the early ontogenetical stages remaining more constant. In this case *Eubora grevei* would be interpreted as a form of *E. bella* which has possibly lived under unfavorable conditions, reducing the strength of the spiral ornamentation of the shell as well as its size; the reduction of the size would apply to *E. woodwardi*, too. The beds of Iquitos would then have to be younger or—if lateral facies variation is assumed—of about the same age as the beds of Pichua/Pebas.

This question cannot be answered without knowledge of the relative position of the fossiliferous horizons of Pichua/Pebas and Iquitos; the author can only point to the possibility that a phylogenetical development useful for a stratigraphical subdivision of the Pebas Formation may exist.

The stratigraphical age of the Pebas Formation, however, cannot be assessed by the genera and species treated here, as neither *Eubora* nor *Toxosoma* nor close allies of them have been encountered outside the Pebas Formation.

PALEOECOLOGICAL IMPLICATIONS

The reassessment of the taxonomic position of the genera *Eubora* nom. nov. and *Toxosoma* Conrad, 1874 has consequences for paleoecological interpretations, as the interpretation of the fauna to be of brackish water character was based in part on the attribution of *Eubora* and *Toxosoma* to the marine family Lacunidae. Here *Eubora* and *Toxosoma* are transferred to the Hydrobiidae which include a large number of freshwater and in part brackish water inhabiting species. Also the form described by ETHERIDGE, 1879, under the two names of "*Assimineia crassa*" and "*Hydrobia dubia*" is removed from these genera which indicate littoral marine conditions (*Assimineia*: soft substrates of the supralittoral; *Hydrobia*: littoral to shallow sublittoral and lagoonal habitats, marine to nearly fresh water) and questionably referred to *Littoridina*.

So the brackish water character of the faunas of the Pebas Formation is considerably reduced as now nearly every species of this Formation may occur in fresh water. Apart from *Eubora*, *Toxosoma*, "*Assimineia*" and

"*Hydrobia*", this applies to species of the families Neritidae and Dreissenidae which were often cited to indicate brackish water but may occur as well in fresh water. Only few arguments remain to make slightly brackish conditions probable: 1) The Bivalve genus *Pachydon* Gabb, 1868 belongs to the family Corbulidae otherwise strictly marine, and has been found in Venezuela in brackish water strata (RUTSCH, 1952). It is improbable that this form which evolved from a marine stock migrated into pure fresh water. 2) The faunal associations of the Pebas Formation are not those of typical fresh water, as large groups of fresh water mollusca (Planorbidae, Ampullariidae, Unionacea) are missing or exceptional. 3) Many shells show circular bore holes. Very similar holes are produced by marine gastropods of the families Naticidae and Muricidae. However, as no form assignable to one of these families has been detected, the origin and thus the significance of the holes is unknown.

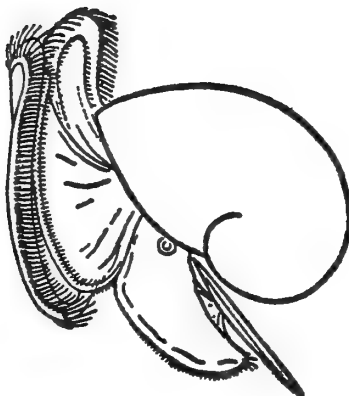
SUMMARY

Summarizing, the salinity of the depositional environment of the Pebas Formation faunal assemblages was probably near fresh water, possibly oligohaline to miohaline (0.05 to 0.5% salinity).

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Gastropod Mimicry by Another Pleustid Amphipod in Central California

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(1 Plate)

THREE EXAMPLES OF MARINE AMPHIPODS which mimic neighboring mitrelliform gastropods have been reported. In southern California Crane (1969) reported the first case where the model, *Alia carinata* (Hinds, 1844), a variably colored columbellid gastropod, was mimicked by the pleustid amphipod *Pleustes platypa* Barnard & Given, 1960. In the same paper Crane reported another unidentified amphipod mimicking a different color morph of *A. carinata* in pholad holes off Point Loma, California. A third example was reported from Friday Harbor, Washington (FIELD, 1974) where the gastropod models were several closely related members of the genus *Lacuna* Turton, 1827. The gastropod mimic was identified as another pleustid amphipod, *Stenopleustes* sp. Experimental evidence at Friday Harbor, Washington demonstrated another example of Batesian mimicry in the eelgrass habitat (FIELD, 1974). Controlled laboratory experiments utilizing common amphipod and gastropod prey items with two fish predators revealed a seven-fold increase in predation over *Stenopleustes* on co-occurring nonmimetic amphipods. FIELD (1974) proposed that by mimicking the conspicuous *Lacuna*, the amphipod realizes a protective advantage and increased survivorship from predatory fish.

It is the purpose of this paper to report another example of apparent Batesian mimicry by a different pleustid amphipod *Pleustes depressa* Alderman, 1936.

During the course of study on an amphipod using gastropod shells (CARTER, 1978) at Diablo Canyon, San Luis Obispo County, two specimens of *Pleustes depressa* were collected from the shallow (-4 m) rocky subtidal habitat. An additional 10 specimens were collected at Morro Bay, San Luis Obispo County during shallow (-3 m) trawling efforts near an eelgrass habitat. All 12 mimicking amphipod specimens exhibited variable colors and patterns specific to the highly variable *Alia* (models) of each habitat. Both specimens from the rocky subtidal habitat were females. The specimens collected during trawls included one male, 7 females, and two juveniles.

The first specimen collected from the rocky subtidal was light tan with a conspicuous dark brown third thoracic segment and urosome. The dark band against the tan background gave the distinct impression of the common banded form of *Alia carinata*. The senior author observed this individual to be associated with a small mass of drifting algae. It was initially believed to be an empty *Alia* shell, possibly inhabited by the amphipod, *Photis conchi-*

Explanation of Figure 1

Alia carinata Model above with Mimicking *Pleustes depressa* below



Figure 1

cola Alderman, 1936. However, when it moved by rapidly crawling across a blade of algae, I thought it was a shell inhabited by a juvenile hermit crab. Repeated attempts to capture "the shell" resulted in the same crawling behavior. At no time did the specimen exhibit a swimming behavior. The specimen was finally captured with a collecting jar and returned to the laboratory where it was identified as *Pleustes depressa*.

A second specimen was collected later in a similar shallow rocky subtidal area and put into a holding aquarium for further observation. In general the behavior of the amphipod was consistent with observations made by CRANE (1969) and FIELD (1974) with ambulatory movements resembling those of a gastropod (slow crawling). Short duration swimming was induced only after prodding with forceps.

The second collected specimen of *Pleustes depressa* compared quite closely with the model *Alia carinata* (Figure 1). The light and dark areas on both specimens are tan and chocolate brown. The color patterns consisting of bands, broken lines and chevrons are very similar between model and mimic. The last 3 or 4 segments on gnathopods and walking legs are white and similar to the cream colored foot and siphon of the model. Although we made intensive searches in the shallow subtidal areas where *Alia carinata* are common, we failed to locate additional mimics.

The second series of 10 specimens was collected in the harbor channel at Morro Bay, a habitat quite different from that of Diablo Canyon. Numerous *Alia carinata* were collected while trawling through shallow eelgrass *Zostera* beds near the harbor entrance. These *Alia* were observed (second author) to differ from the open coast forms as they were neither chevroned nor banded, but predominantly uniform dark brown to black. The 10 specimens of *Pleustes depressa* again compared closely with the model, the body being dark brown to black with cream to white legs resembling the foot and siphon of *Alia*. They closely resembled the gastropod models and were not detected until they extended their legs to move across the deck of the boat.

BARNARD (1969) suggested that Point Conception represents a zoogeographical boundary which generally separates the adults of the two species of *Pleustes*; *P. depressa* found to the north in Central California and *P. platypa* in

southern California. BARNARD (*op. cit.*) did note that juvenile specimens of *P. depressa* were found at La Jolla, California and their occurrence was rare. Additionally, mimicking forms of *P. depressa* and *P. platypa* appear to be segregated by habitat. CRANE (1969 and personal communication, 1978) collected *P. platypa* from drifting kelp *Macrocystis* while BARNARD (*op. cit.*) and BARNARD & GIVEN (1960) recorded specimens at depths of 15.4 m and greater. *Pleustes depressa* has only been observed in near-shore intertidal and subtidal areas (ALDERMAN, 1936; HEWATT, 1946; BARNARD, *op. cit.*).

BARNARD (1969) observed that the "southern species may be taxonomically linked with those of the Arctic-boreal in a common epigenotype." Observations by CRANE (1969), FIELD (1974) and data presented herein tend to support this evolutionary speculation with ecological evidence.

ACKNOWLEDGMENTS

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Early Development of *Mytilopsis leucophaeata*

(Bivalvia : Dreissenacea)

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(1 Plate)

SEVERAL KEYS HAVE BEEN PUBLISHED for identification of bivalve larvae based on characters of the larval shell, or prodissoconch (CHANLEY & ANDREWS, 1971; LOOSANOFF, DAVIS & CHANLEY, 1966). However, none describe *Mytilopsis leucophaeata* (Conrad, 1831), an estuarine species distributed along the North American east coast from New York to Florida and from Texas to Mexico (ABBOTT, 1974; EMERSON & JACOBSON, 1977). The objective of the present study was to describe the development of larval and juvenile *M. leucophaeata*.

In early 1975, I monitored the abundance of bivalve larvae in a man-made embayment on Virginia Key, Miami, Florida, supporting a population of bivalves composed almost exclusively of *Mytilopsis leucophaeata*. No other adult bivalves were observed and greater than 99% of all larvae collected and reared through metamorphosis in the laboratory were later identified as *M. leucophaeata*. Natural (filamentous algae) and artificial (cotton thread) spat collectors were sampled for metamorphosing bivalves. Tidal flushing was restricted with salinities decreasing from 22‰ to 8‰ after late spring rains. Heaviest set of spat occurred two weeks after the onset of this annual rainy season. Temperatures varied from 13°C (January

to 30°C (July), averaging 26°C during spatfall. In the spring of 1976, sexually ripe adults exposed in the laboratory to 35°C seawater (10‰) for 20 minutes spawned within one hour of treatment. Larvae were reared through metamorphosis at three salinities (10, 24 and 32‰) using techniques commonly applied in the culture of bivalve larvae (LOOSANOFF & DAVIS, 1963). Serial samples of both naturally set larvae and juveniles (1975 material) and laboratory cultured larvae and juveniles (1976 material) were cleaned in a buffered sodium hypochlorite solution (see CARRIKER, 1979) then examined on an AMR-900 scanning electron microscope.

Though the effects of the three salinities were not significant on either the timing of, or the size at, metamorphosis ($P > 0.05$), it is interesting that these brackish water bivalve larvae were capable of growth to metamorphosis at near-oceanic salinities (32‰).

Characteristics of the hinge line are used to differentiate bivalve species both as larvae and adults (REES, 1950; LUTZ & JABLONSKI, 1978; SIDDALL, 1978). Serial development of the hinge line in *Mytilopsis leucophaeata* is shown in Figure 1. Using the terminology of CHANLEY & ANDREWS (1971), *M. leucophaeata* develops "knobby"

Explanation of Figures 1 and 2

Figure 1: SEM photomicrographs of hinge lines of *Mytilopsis leucophaeata* at two times prior to metamorphosis: a) 2 days after fertilization (DAF); shell length = 74 µm; b) 6 DAF; shell length = 180 µm; and at three times subsequent to metamorphosis: c) 12 DAF: maximum shell dimension = 270 µm; d) 18 DAF:

maximum shell dimension = 375 µm; e) 28 DAF: maximum shell dimension = 500 µm; showing shelf under the umbo

Figure 2: SEM microphotograph of juvenile *Mytilopsis leucophaeata* (0.5 cm maximum dimension) (a) with pits randomly dispersed anterior to pallial line; and (b) a magnified view of pit (3 µm in diameter)

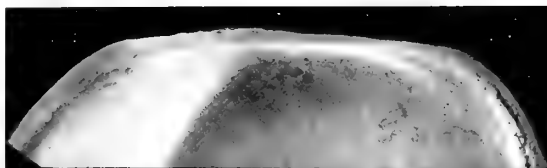


Figure 1a

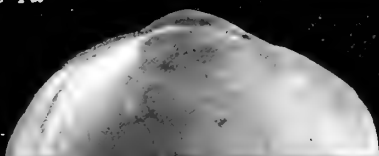


Figure 1b

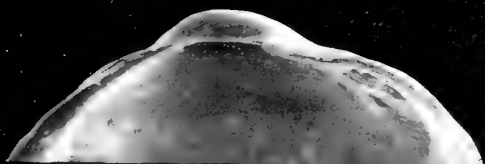


Figure 1c

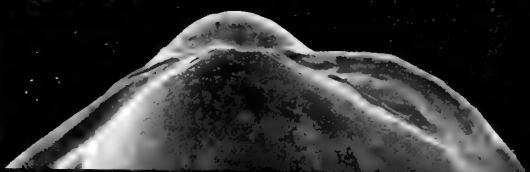


Figure 1d

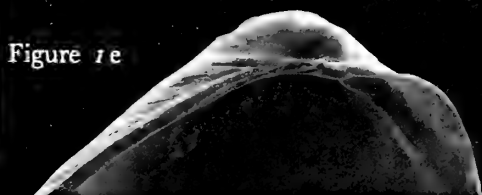


Figure 1e

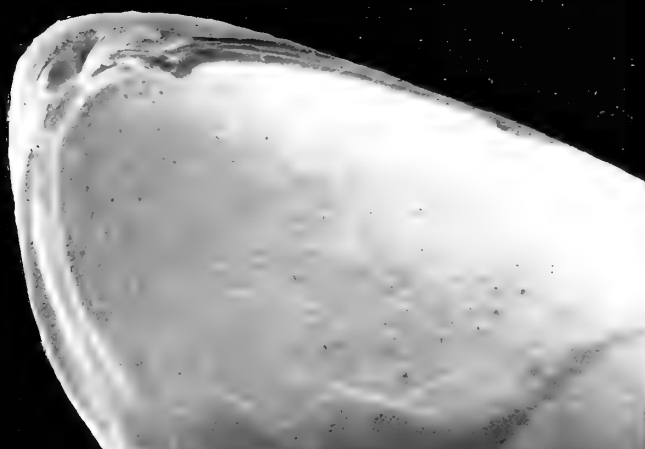


Figure 2a

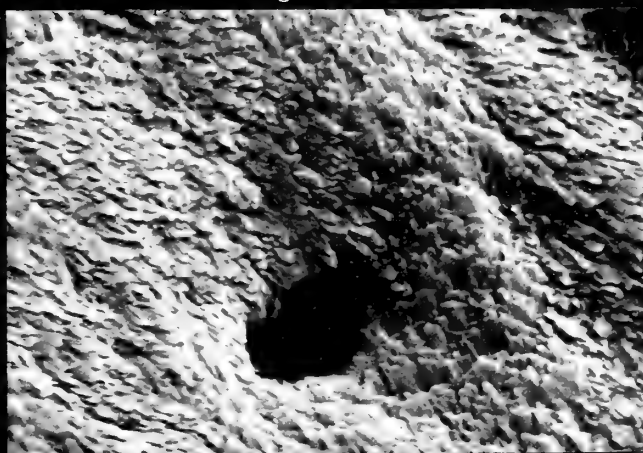


Figure 2b

umbones which became "skewed" anteriorly following metamorphosis. At 26° C, larvae fed a mixed phytoplankton diet (*Isochrysis galbana*, *Monochrysis lutheri* and *Tetraselmis suecica*) metamorphosed 6 to 8 days after fertilization at a mean shell length (parallel to the hinge line) of 210 μ m ($n=25$). Neither larvae nor juveniles of *M. leucophaeata* possess hinge teeth at any stage. The "triangular tooth" referred to in ABBOTT's (1974) description of *M. leucophaeata* is a projection of the shelf near the beak, not to be confused with hinge teeth. Because the adult ligament is broad, the shell presumably does not require teeth for stabilization of the opening and closing motion of the valves. For the adult population sampled, mean maximum shell dimension was 2.2 cm ($n = 125$).

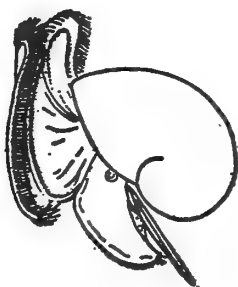
Figure 2 shows a typical juvenile (0.5 cm maximum shell dimension). Evenly dispersed and uniformly shaped tubules penetrate the inner calcareous crossed-lamellar layer typical of the Dreissenacea (KENNEDY, TAYLOR & HALL, 1969a). These tubules range in diameter from 3 to 5 μ m and should not be confused with the very small tubule-like structures occurring in mytilids (an order of magnitude smaller). The tubules of *Mytilopsis leucophaeata* are uniformly distributed in, and restricted to, the older regions of the shell bounded by the pallial line. This distribution suggests a secondary origin for the tubules (KENNEDY, TAYLOR & HALL, 1969b). In their brief review of tubulate bivalve shells, KENNEDY *et al.* (1969b) state that these tubules penetrate the periostracum. Such was not the case in the material examined in the present study. The tubules of *M. leucophaeata* first appear in metamorphosed juveniles (0.5 mm maximum shell dimension) and are seen in individuals of all larger sizes.

To summarize:

- (1) in the population of *Mytilopsis leucophaeata* studied, gamete release consistently occurred as salinities decreased during the annual rainy season;
- (2) settlement of spat peaked 2 weeks after gamete release in natural populations; in the laboratory at 26° C, well fed larvae metamorphosed in 6 to 8 days;
- (3) *Mytilopsis leucophaeata* larvae and post-larvae are euryhaline, capable of development to metamorphosis at 10 to 32‰;
- (4) neither larvae nor older stages of *Mytilopsis leucophaeata* possess hinge teeth;
- (5) shells of juvenile and older *Mytilopsis leucophaeata* are tubulate; tubules are restricted to the older shell regions bounded by the pallial line and do not penetrate the periostracum.

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Fish Predation on Pulmonate Limpets

BY

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(2 Text figures)

FISHES MAY BE IMPORTANT PREDATORS on invertebrates in tropical marine systems (BAKUS, 1969) either because they inadvertently remove invertebrates while browsing on algae (RANDALL, 1974; VINE, 1974; DAY, 1977) or because they focus specifically on invertebrate prey (HIATT & STRASBURG, 1960). In this note I present indirect evidence that loss of 21% of a population of the intertidal pulmonate limpet *Siphonaria normalis* at Enewetak Island, Enewetak Atoll, Marshall Islands resulted from selective removal by fishes during a spring high tide. Mortality was size-specific and altered the size structure of the population.

Siphonariid limpets occupy specific home sites on rocks (COOK, 1969) when they are not grazing on microscopic algae (VOSS, 1959). Home sites of individuals on soft rocks are marked by "scars," depressions whose dimensions are the same as limpet basal dimensions. Because *Siphonaria normalis* are always "at home" at dead low tide (1 homing failure out of 133 grazing excursions) and limpets which do wander stay close to scars and can be readily recognized by visible gaps between shell margins and the rock, the presence of empty scars at low tide coupled with a lack of "extra" limpets on the rock is evidence of mortality.

Such a combination of events occurred in a *Siphonaria normalis* population located on beachrock on the lagoon side of Enewetak Island. During one late afternoon spring tide (1.5 m above 0 datum, October 6, 1975), four of the 19 original residents of a 25 x 25 cm quadrat disappeared. On the next daytime low tide, I found no "extra" limpets and discovered that empty scars were distinctively marked with grooves extending from the adjacent rock down into scars (Figure 1). Within a nearby 50 x 50 cm area, similar marks were associated with the empty scars of 10 of 49

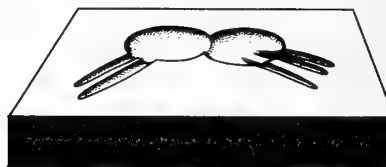


Figure 1

Two adjacent empty limpet scars marked by prominent grooves; each scar is about 8 mm in length

residents, while all of another 50 empty scars on the rock outside of these two areas were marked. Marks were rare on the rock between scars (<10% of the total number found).

Bits of limpet tissue present in two of the marked scars confirmed that limpet mortality had indeed occurred. Although the rock in the vicinity of two additional animals was also marked, these animals escaped removal. All empty scars and marks were obliterated by algal growth within 2-4 days.

Marks were of an appropriate size and spacing to have been made by the canine teeth of a large wrasse such as *Coris aygula* (J. Randall, personal communication). This species is found at Enewetak in shoal areas, as well as deeper water, and often eats mollusks (J. Randall, pers. comm.). Two other possible predators, the golden plover *Pluvialis dominica* (A. Kohn, pers. comm.) and the muricid gastropod *Thais armigera* (Menge, 1973), can be excluded. Plovers are not likely to dive to reach limpets submerged during spring high tides. Predatory snails were not

seen in the area either before or after limpet loss and in any case would not have left grooves on the rock.

Large limpets were clearly more affected than were smaller individuals. The mean length of empty scars (and therefore of former residents) was significantly greater than the mean length of survivors (Figure 2, t-test, $P < 0.001$). Proportions of scars in the size categories 4-7 mm and 8-12 mm were significantly different from proportions expected if limpets had been removed according to initial abundance (chi-square goodness of fit, $P < 0.05$). One reason for the relatively better survival of small individuals may be inaccessibility: the two survivors mentioned earlier were small (<6 mm) individuals whose homes were located at the bottoms of small pits in the rock. Predation resulted in a small but significant decline in the mean length of limpets within the two quadrats (from 6.7 mm to 6.1 mm, t-test, $0.05 > P > 0.02$).

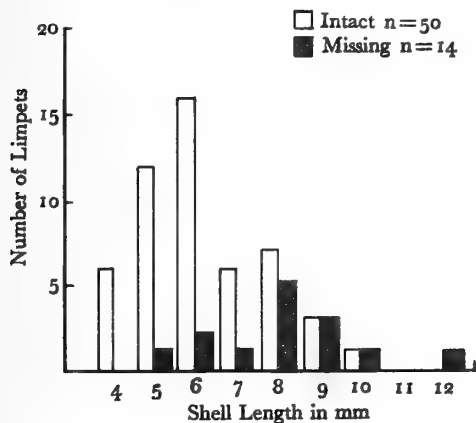


Figure 2

Size comparisons of intact limpets on scars and unoccupied grooved limpet scars following fish predation

Information on how often fish predation affects tropical limpet populations over the long term is lacking. Although such predation is one explanation for the scarcity of large

Siphonaria normalis at Enewetak (less than 1% larger than 8 mm, MENGE, 1973; less than 1% larger than 8 mm at another study site, Cook, unpublished), alternative explanations are possible. These include size-specific predation by *Thais* (MENGE, 1973) or shorebirds, or both, as well as periodic catastrophic mortality of all limpets followed by recruitment and growth of recruits into small to medium sized limpets.

ACKNOWLEDGMENTS

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Intermediate Forms and Range Extension of *Pedicularia californica* and *Pedicularia ovuliformis*

BY

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(3 Text figures)

TWO FORMS OF *Pedicularia* are known from the California coast: *P. californica* (Newcomb, 1864) and *P. ovuliformis* (Berry, 1946). In comparison, the former is slightly larger, irregular, with simple outer lip, and lighter in color. The latter is uniform in size and shape, with a heavy

dentate outer lip, crenulate outer margin, and a rather intense rose-pink color. Heretofore, no specimens intermediate between these two forms or their existence north of the Farallon Islands have been known.

The October 1978 scuba expedition to Cordell Bank,

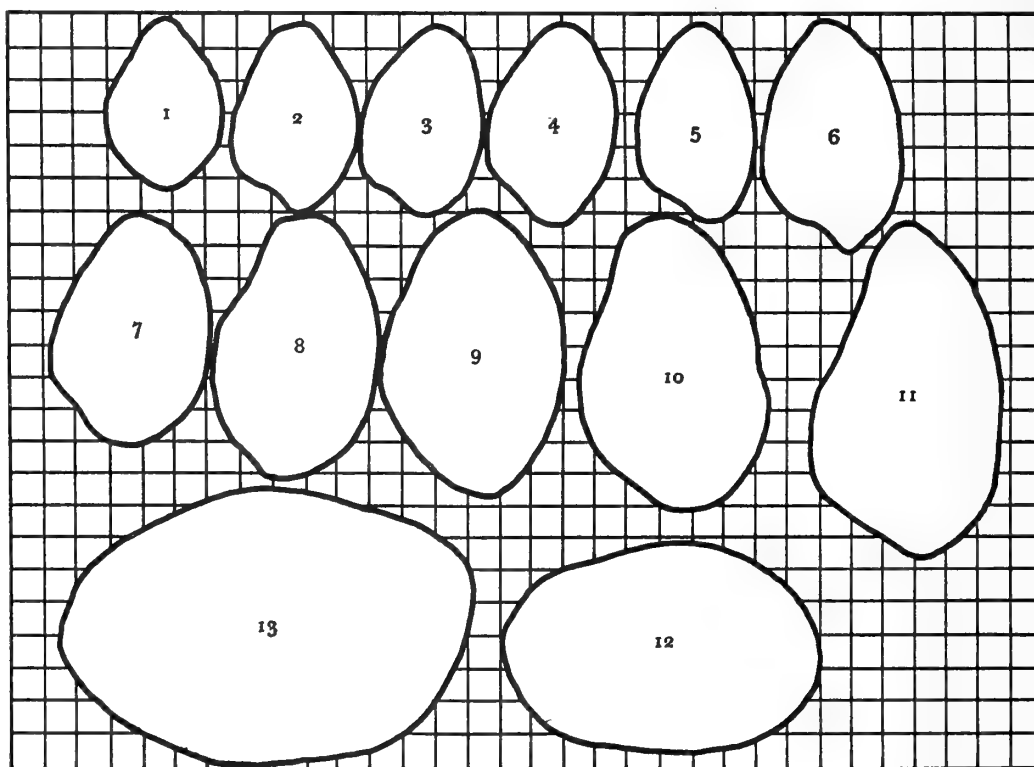


Figure 1

Outlines of the 1978 Cordell Bank *Pedicularia*, viewed dorsally. The grid spacing is 1 mm, and the numbering corresponds to the entries in Table 1

30 km W of Point Reyes, carried out by the author and colleagues (SCHMIEDER, 1979) yielded 13 specimens of *Pedicularia*, most collected live among abundant hydrocoral (*Stylantheca porphyra*), thus extending the range to Latitude 38° N. The specimens were collected in clear water (visibility ~18 m, temperature ~14° C) at depths of 39.6 to 46.8 m, from a tiny pinnacle at Latitude 37°-59'30", Longitude 123°24'30", now known as Craines Point. Figure 1 shows outlines of the 13 specimens.

Among the specimens are several of the 2 well-known forms, plus several of intermediate character. One in particular exhibits both the classic simple lip of *Pedicula-*

ria californica, and, within the aperture, the classic dentated lip of *P. ovuliformis*. Remnants of the crenulate outer margin can be seen on the exterior, well below the aperture. The exterior color is very similar to that of *P. ovuliformis*, except that the shell added beyond the crenulations is lighter, close to that of *P. californica*. Figure 2 shows 2 of the specimens, one clearly *P. ovuliformis* and the other the intermediate form.

Other specimens in the collection show similar but less complete suggestions of both forms. Several have an easily identified smaller, darker "core," of the size and color of *Pedicularia ovuliformis*, surmounted by a lighter, more open, simple labrum, giving them the overall approximate appearance of *P. californica*. Microscopic examination shows evidence of overgrowth of a flat, heavy labrum, probably dentate, and possible remnant of interior overhang of the flat lip of *P. ovuliformis*. Table 1 gives the significant characters of these specimens and in Figure 3 is plotted the width vs length, which is seen to be approximately linear.

It is therefore not unreasonable to conclude that there is probably only one species of *Pedicularia* in Northern California, that *P. ovuliformis* is a phase leading to *P. californica* by partial resorption of the flat dentate labrum and simultaneous extension of a simple labrum, with size increase and reduced pigmentation. This possibility was also considered by BERRY (1946), who rejected it in favor of defining *P. ovuliformis* as a new species.

A possible explanation for these facts is the following: In the colder water further north, the growth rate is probably slower than in more southerly areas where *Pedicularia* is more commonly found. Thus, more time would

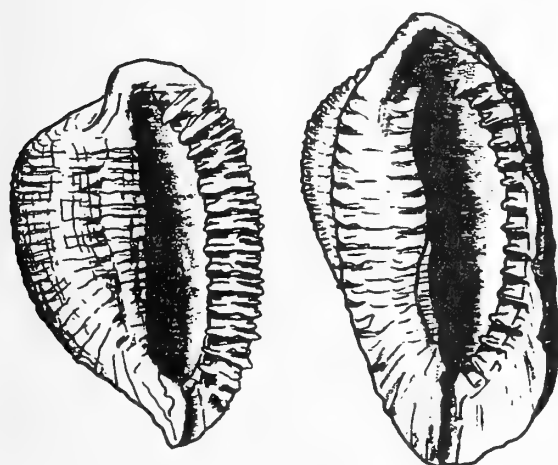


Figure 2

Drawings of two specimens, *Pedicularia ovuliformis* (No. 5), and the intermediate form (No. 6). Drawn from photographs

Table 1

Pedicularia from Cordell Bank 1978

No.	Length (mm)	Width (mm)	State	Dentation	Crenulation	Remarks
1	5.2	3.4	live	rudimentary	none	
2	5.8	3.7	dead	partial	none	
3	6.0	3.6		partial	rudimentary	<i>P. ovuliformis</i>
4	6.1	4.0		complete	partial	<i>P. ovuliformis</i>
5	6.2	3.5		complete	complete	<i>P. ovuliformis</i>
6	6.9	4.3	live	complete	residual	Intermediate form
7	6.9	4.9	dead	ambiguous	ambiguous	White; aperture unusual
8	7.9	5.0	live	none	none	<i>P. californica</i>
9	8.5	5.6	live	none	none	<i>P. ovul.</i> core, w/chg. of growth at junction
10	9.1	5.9	dead	rudimentary	none	
11	10.0	6.3	dead	ambiguous	partial	Lips somewhat thickened
12	10.4	6.0	live	none	none	Lips slightly thickened; has <i>P. ovul.</i> core
13	12.4	8.6	live	none	none	Lips extremely thickened; very heavy, several phases.

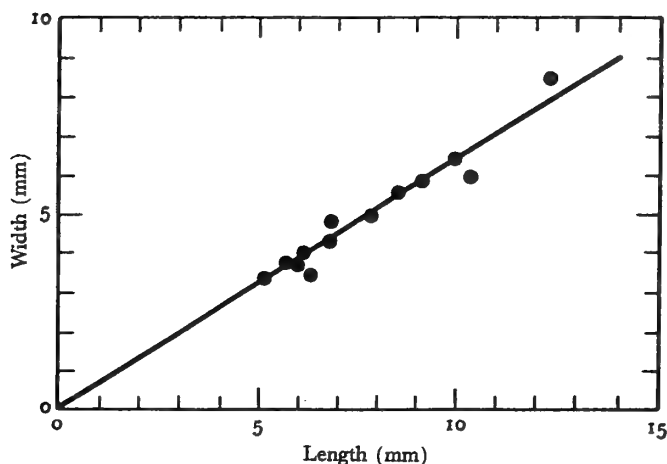


Figure 3

Width vs. length of the 13 specimens

be spent in making the transition from *P. ovuliformis* to *P. californica*, and the probability of finding the intermediate form would be correspondingly higher, accounting for its discovery at Cordell Bank. The individual reaches maturity as *P. ovuliformis*, spending some time on its color-encrypting substrate *Stylantheca*. Then, in response to an environmental change (which may actually be a change

in the substrate occasioned by a more primitive cause such as temperature), it suddenly puts on a growth spurt. In order to contain the animal, the outer lip is rapidly extended, leaving the flat, dentate margin as an interior shelf, which is then resorbed to clear the passage (resorption is known in other species of *Pedicularia*). Irregularity in form is due to the rapidity of growth – if conditions returned to the earlier state, it might well construct another flat, heavy, dentated outer lip. There is some evidence of this last, since the largest (and presumably oldest) specimens in the Cordell Bank collection have greatly thickened lips, and retain irregular forms.

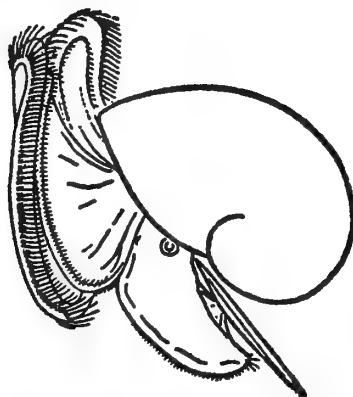
These specimens have been deposited in the collection at the California Academy of Sciences, San Francisco, California, accession number 60363.

ACKNOWLEDGMENT

It is a pleasure to acknowledge the considerable help in this study by Barry Roth of the California Academy of Sciences.

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Helix aperta Introduced in Richmond, California

(Mollusca : Pulmonata)

BY

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AND

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(1 Text figure)

IN MARCH 1979, Mr. Gordon E. Bergman and his daughter Katherine discovered an infestation of the European and North African snail, *Helix aperta* Born, 1778, in an industrial district of Richmond, Contra Costa County, California. During a period of intermittent rains, the snails were observed to be numerous, crawling actively during the day. Also in March, Mr. Sterling Bunnell brought specimens collected by Mr. and Miss Bergman to the California Academy of Sciences for identification. From early April to May 1979 the authors investigated the site of infestation – a region of artificial fill along the south side of Point Isabel, on the east shore of San Francisco Bay in the southern part of Richmond.

We found *Helix aperta* to be common south of Central Avenue (Figure 1), from near the base of the Central Avenue overpass over Hoffman Boulevard to the vicinity of a sewage pumping station approximately half the distance along the south shore of Point Isabel, and from the south edge of the paved roadway to the margin of the filled land. The infested area is entirely on artificial fill emplaced between 1949 and 1968, according to editions of the U. S. Geological Survey Richmond Quadrangle (7.5 Minute Series, Topographic). The ground is flat and weedy with large clumps of the shrub, *Baccharis pilularis* var. *consanguinea* (DC.) C. B. Wolf. The soil is clayey and gravelly, rather extensively tunnelled by rodent burrows.

Helix aperta shells were present among weeds and in the litter under *Baccharis* clumps. Living individuals were most common on and under rubbish on the ground. The greatest concentration was in the area south of the foot

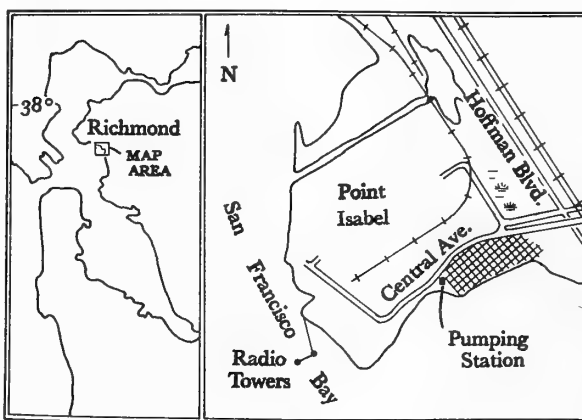


Figure 1

Point Isabel, Richmond, California.
Crosshatching indicates presence of *Helix aperta*

of the Central Avenue overpass, which is a site of casual dumping of garden clippings and household refuse. A few living specimens were observed in rodent burrows. During a visit May 4, living juveniles (to about 1 cm diameter) were found on the leaves of thistle (*Cirsium*) and sow-thistle (*Sonchus*) as much as 30 cm above the ground. Dead snails in various stages of decomposition indicate that the species may have been established for more than one year. Associated mollusks included *Helix aspersa* Müller, 1774, *Milax gagates* (Draparnaud, 1801), *Deroceras*

caruanae (Pollonera, 1891), and *D. reticulatum* (Müller, 1774), all introduced; and *Punctum conspectum* (Bland, 1865), native to California but probably introduced to this site.

No *Helix aperta* were observed north of Central Avenue in a weedy field with fennel plants (*Foeniculum vulgare* Mill.), in a slough with pickleweed (*Salicornia*) north of the overpass, nor along the Bay shore east of the Point Isabel peninsula. A region of *Baccharis* bushes near the northwest end of Point Isabel yielded only *Helix aspersa*.

The largest specimen collected, an empty shell, measures 26.4 mm in height and 30.4 mm in maximum diameter, equal to the size attained in Europe; it has 3.25 whorls. Shells of most living specimens collected are about 20 mm in height and 22 mm in maximum diameter, with about 3.25 whorls, and probably represent a single age class.

Helix aperta was first reported in California by GAMMON (1943); he described an infestation discovered in San Ysidro, San Diego County, in April 1941, where the snails were abundant on streets after showers. Preliminary surveys in 1941 showed the species to be present over at least 10 blocks and many acres of pasture and river bottom land in San Ysidro. Further survey during the following winter and spring revealed it in several additional blocks in San Ysidro and over many acres around dumps in the vicinity. Gammon estimated that approximately 500 acres were then infested. Some damage to home gardens was reported. The species was still present and was causing agricultural damage in 1951 (CAMPBELL, 1953). The San Ysidro infestation was the only occurrence reported by HANNA (1966) in his survey of introduced mollusks of western North America. We were advised by Dr. Tokuwo Kono (*in litt.* 26 April 1979) of the California Department of Food and Agriculture that that agency has no other records of the species' establishment in California.

DUNDEE (1974) noted museum lots of *Helix aperta* from New Orleans, Louisiana, and Nahant, Massachusetts. She stated that, as of the date of her writing, the species was no longer present in New Orleans. HARRY (1948) reported that living, imported *H. aperta* were sold in open baskets in Louisiana but that the species was not known to have established itself.

Helix aperta is native to the Mediterranean region. It is said to be chiefly a ground snail, rarely climbing to any height on plants (FRÖMMING, 1954). In its countries of origin it is found principally under foliage and stones, often on cultivated land. GAMMON (1943) stated that it is very active during the rainy season but soon burrows in soil to depths as great as 6 inches (15 cm). Estivation

takes place in an earthen cell, behind a thick, convex epiphragm, with re-emergence following autumn rains. The burrowing habit makes it difficult to determine the extent of an infestation and hampers eradication.

Two modes of introduction to the Richmond site seem possible: (1) the species was brought in with soil used for artificial fill, or (2) it was present on garden debris dumped in the area. The burrowing habit of the snail makes transport in soil a possibility. On the other hand, the observations that, as far as could be determined, distribution is limited by a paved road and density is greatest near a dumping site suggest a more recent introduction, probably with horticultural rubbish. This implies that *H. aperta* may be established in gardens in one or more of the neighboring communities.

There is a continuing potential for introduction. Between July 1, 1973, and September 30, 1977, *Helix aperta* was intercepted 17 times by the U. S. Department of Agriculture Animal and Plant Health Inspection Service (U. S. Department of Agriculture, 1979). The species was intercepted at ports in Louisiana, New York, and Texas, in or on baggage, stores, and cabbage. Infested shipments originated in France, Greece, Italy, and Spain. Between 1964 and 1972, additional interceptions were made in cargoes originating in Argentina, Australia, the Azores, Belgium, England, Haiti, Ireland, Mexico, Netherlands, and Peru, as well as most of the countries around the Mediterranean (DUNDEE, 1974; R. D. Munkittrick, personal communication, May 1979). In 1974, permits were issued to 3 importers allowing entry of *H. aperta* into the New York City metropolitan area for local sale (R. D. Munkittrick, personal communication, May, 1979).

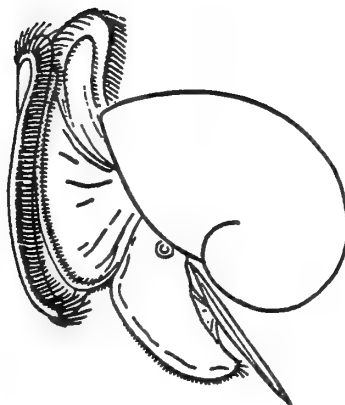
Point Isabel was formerly a locality for the native snail *Helminthoglypta contracostae* (Pilsbry, 1895) (PILSBRY, 1927, 1939). ALLYN G. SMITH (*in* PILSBRY, 1939: 102) reported *H. contracostae* as "a shell of the mud flats along the shore on the east side of San Francisco Bay in the general vicinity of San Pablo. . . . At these places definite colonies are to be found under low bushes, in tall grass, and under *Salicornia*." The nominal species *Epiphragmophora arnheimi* Dall, 1896 — now regarded as a synonym of *H. contracostae* — was based on specimens from the San Pablo area. No *Helminthoglypta* were observed in the course of this investigation, and, given the extent of habitat alteration along this part of the Bay shore, we consider it unlikely that *H. contracostae* survives in the Point Isabel area. SMITH (1970: 41) stated, "the habitat for the race *arnheimi* on the east side of San Francisco Bay has been completely destroyed by industrial expansion."

ACKNOWLEDGMENTS

We are grateful to R. D. Munkittrick, U. S. Department of Agriculture, for supplying literature and interception records and T. Kono, California Department of Food and Agriculture, for data on the distribution of *Helix aperta* in California.

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Spiroglyphus and *Stoa*, Taxonomic Problems in the Vermetidae

BY

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(1 Text figure)

IN 1961, WHEN I WAS PROPOSING a reclassification of the family Vermetidae, I could not come to a clear resolution of the problems with two generic names. Reviewing those problems now, I am reminded of the words of a Dutch zoologist, M. M. SCHEPMAN (1908: 183), who said caustically of the vermetids that they are "the most disagreeable among gastropods to deal with. The extreme variability ... and the often vague descriptions render ... impossible ... safe identifications." This applies, indeed, to *Spiroglyphus* Daudin, 1800, and *Stoa* De Serres, 1855. I advised, in 1961, setting *Spiroglyphus* aside as a *genus dubium*, although it was a taxon long considered molluscan, for I found there was a possibility the original material might have been annelid instead. I felt the name should be revived only if authentic type material could be brought to light or a plausible neotype specimen selected. The second name, *Stoa*, I dismissed as not applying to the Mollusca, on the advice of the paleontologist Dr. B. F. Howell, who was revising the fossil Annelida for the "Treatise on Invertebrate Paleontology." He thought that *Stoa* was undoubtedly a tubicolous annelid. However, when that volume of the "Treatise" was published, Howell did not list the name *Stoa* because he found no fossil records of it. More recently, in a systematic reference work on polychaete annelid genera, FAUCHALD (1977: 152) cited *Stoa* under the serpulid family Spirorbidae, but only as a genus that is "invalid" and "indeterminable." The problem of *Spiroglyphus* remains today as enigmatic as ever, and *Stoa* floats ghost-like, unclaimed in either Mollusca or Annelida.

This paper is an attempt to review the problems for both of these taxa and to assess the consequences of alternative courses of action.

The generic name *Spiroglyphus* Daudin, 1800, comprised two species, *S. politus* and *S. annulatus*. Only the latter was figured (see Figure 1). Both were said to have tubular shells, irregularly coiled, entrenched on the surface of other shells, *S. politus* on pectens and pinnae in

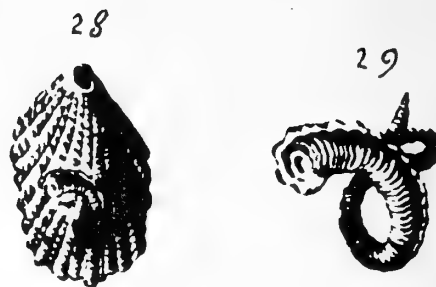


Figure 1

Figures 28 and 29 from DAUDIN, 1800, "Recueil de mémoires et de notes sur des espèces inédites ..."

Figs. 28-29. *Spiroglyphus annulatus*

28. Grandeur naturelle, sur une fissurelle

29. Grossi, et détaché.

the Indian Ocean area and *S. annulatus* on patellas and fissurellas, also of the Indian Ocean. The figure shows a specimen attached to what appears to be a strongly ribbed keyhole limpet. The entrenched shell is well portrayed, showing the lamellar growth increments that are characteristic of many vermetids. However, the initial whorls are shown as straight, a characteristic of tube worms, whereas vermetid gastropods have helical coiling in the initial whorls. The shell to which Daudin's specimen was attached is rather sketchily drawn. He had not seen the soft parts of either of the two species, and his discussion shows that he was only dimly aware of how tube worms and mollusks might differ.

The name *Stoa* was proposed for a new genus of tubicolous annelids by De Serres in 1855. He had three species, all illustrated, but he had only the shells for the first two, *S. ammonitiformis* and *S. spirulaeformis*. For the

third one, *S. perforans*, he figured also an operculum. He characterized the genus as having an irregularly coiled shell, the last whorl often detached from the first and even prolonged into a straight tube; the aperture oval, ending in a solid, calcareous, conic operculum formed of three small circular bands, concave externally, diameter 2 to 3 mm. The illustration of this operculum shows it as having a steeply conic profile, with a notch on the outer edge, unlike that of any known species of vermetid. De Serres' statement, made twice, that the operculum is calcareous led Dr. Howell and later authors to infer that *Stoa* was indeed an annelid. TRYON (1886) reprinted De Serres' figures (plt. 51, figs. 48-49; plt. 52, fig. 54; plt. 54, figs. 84-86).

Gray in 1840, in a synopsis of the contents of the British Museum, picked up Daudin's *Spiroglyphus* for use in Mollusca, family Vermetidae, alongside *Vermetus*, which Daudin had also described and had correctly considered as gastropod. The first malacologist to make extensive studies of the family was O. A. L. Mörch, who published a series of papers in the years 1859 through 1862. Although in general Mörch was a careful observer, his discussions were sometimes ambiguous. He recognized *Spiroglyphus* as a genus, coordinate with a genus *Siphonium*, which he dated from Gray, 1850, and he made *Stoa* a synonym of both. The fortunes of *Siphonium*, a name that was invalid because preoccupied by *Siphonium* Link, 1807, need not be pursued here. In synonymizing *Stoa* under *Siphonium*, Mörch commented: "M. de Serres has established a genus of 'Annelides sedentaires tubicolés,' under the name *Stoa*, chiefly on account of their habit of burrowing a bed in the surface of other shells, exactly corresponding to the genus *Spiroglyphus* of Daudin. Both authors have mixed together species of two very different genera, the one with a concave, the other with a thick, convex operculum; but as Daudin has selected for illustration of his genus a species with an operculum of the latter kind, I regard the represented species as the type ..." (MÖRCH, 1861: 152). On *Stoa* he said (*ibid.*, p. 153): "A conical operculum, which is solid and calcareous, seems ... unnatural and without analogy among the Mollusca and Annelida ... The last whorl of the operculum terminates abruptly at the edge ... which I have never seen so strongly expressed, neither have I seen an operculum of the high conical shape figured. ..." Apparently, though, he did accept *Stoa* as molluscan rather than annelid.

Despite having synonymized *Stoa*, Mörch used the name subgenerically under *Siphonium* for 6 species. Nowhere did he categorize the difference between *Siphonium*, s. s., and *Stoa* nor cite a type species for either (in fact, the selection of *S. annulatus* as type of *Spiroglyphus* was one

of the few times in all his published work that he used the word "type"). His basis for including species under *Stoa* is not clear; he reported the operculum as unknown in two, nearly flat in one, and concavely conic in three. The first species he listed was *Siphonium (Stoa) politum* (Daudin), under which he synonymized, because of similar wording of the descriptions, *Stoa perforans* De Serres. It is this latter that has the steeply conic operculum.

In a discussion of the genus *Spiroglyphus*, MÖRCH (1862a: 326) again cited *Stoa* as a synonym and said, "The shell ... is so similar to that of *Stoa* that it can only be distinguished by the operculum, which is convex outside, flat inside, with a central cylindrical wart. ... The colour varies ... from bright purple to nearly black, and the surface from nearly flat to very convex."

The next malacologist to deal with these names was TRYON (1886: 163-ff.). As Tryon was a lumpner, he demoted many of Mörch's units to lower rank but followed his arrangement in the main. He, too, synonymized *Stoa* with *Siphonium* ("in part") and *Spiroglyphus* ("in part"). Mörch's subgenus *Dendropoma* he ignored as a "section." The name *Stoa* then virtually disappeared from the literature until 1939, when J. R. leB. Tomlin used it subgenerically for a South African vermetid, *Vermetus (Stoa) corallinaceus* (reallocated by later authors to *Dendropoma*). Tomlin did not diagnose or cite a type species for the subgenus. *Spiroglyphus*, however, continued in use in Mollusca – although confused with annelids by certain Californian paleontologists – until 1960.

This, then, is the historical background for my recommendations in 1961. No one since has put in a brief for resuscitating *Stoa*, but at least two authors (MORRISON, 1968; ABBOTT, 1974: 99 - 101) have risen to the defense of *Spiroglyphus* on the basis of priority. I would like here to point out the various alternatives and consequences.

First and most obvious step is search for original type material. When I inquired of Dr. Édouard Fischer-Piette of the Paris Museum, who had been successful in recovering Adanson's lost collection, whether the Daudin specimens might be at Paris, he replied that not only were they not in the Paris Museum but that he had no idea of how to start a search. Obviously, an outsider would stand little chance of making this discovery. De Serres' specimens were stated to be in the collections of the Université de Montpellier. Through a French colleague, M. Jacques Laborel, I was put in touch recently with the curator there, Mlle. F. Cassagne-Mejean, who promised not only to search for the material but to send photographs if it were found. Nothing, however, was forthcoming, and we must conclude that this material is lost.

The problem of *Spiroglyphus* is more complex than appears on the surface. Not only is there an open possibility

that the original specimens were annelids but also that the concept that developed of it as a mollusk might have been unjustified. Authors have taken Mörch's statements at face value without realizing that he was making judgments based only on his personal experience. Discussing *S. annulatus*, which he made the type species, he quoted Daudin's statement that it occurred on patellas and fissurellas of the Indian Ocean, and then said (1862a: 330-331): "The represented species is probably *Fissurella barbadensis* Gm." Later authors (e.g., MORRISON, 1968: 45) disregard the "probably" and identify the shell on which the supposed vermetid is shown as *F. barbadensis* Gmelin, 1791, a Caribbean species. One wonders whether they tried actually laying a Caribbean *Fissurella* alongside Daudin's figure. Either Daudin omitted the entire anterior half of the supporting fissurellid and showed only the part behind the orifice or else he drew the shell tilted but the entrenched specimen normally. In either case, he failed to show the radiating ribs accurately, and the proportions seem inconsistent. Had not Daudin cited "fissurelles," I would even suggest that the supporting shell might be one valve of a bivalve that had been perforated by a drill-shell. Although fissurellids are more common in the Caribbean, there are some species of that group in the Indo-Pacific area, and to my eyes a figure labelled "*Diodora jukesii* (Reeve)" from northwest Australia, in "Selected Shells of the World Illustrated in Colour," by SHIKAMA & HORIKOSHI, 1963: plt. 5, fig. 12, is a better match than any figure or shell of a Caribbean fissurellid that I have been able to find. I feel that Daudin's stated locality should be taken seriously unless there is compelling evidence to the contrary.

Mörch's characterization of the morphology of *Spiroglyphus annulatus* really is based on his observation of Caribbean material. He was aware of only one species of "*Spiroglyphus*" there, with a convex purple-black operculum, flat on its inner surface except for a central mamilla. Under *S. annulatus* he synonymized two Caribbean forms, *Vermetus irregularis* and *V. corrodens*, both of Orbigny, 1842 – described from Martinique, the type material now in the British Museum. Actually, there are in the Caribbean three species of entrenching vermetids, each with a distinctive operculum, only one of which is convex. The second Caribbean form has a flat operculum, and the third has one that is concave and horn-colored, with an orange spot on the central mamilla.

What the Indo-Pacific counterpart has for an operculum is an open question. I have seen material from Vietnam that, for shell features, matches Daudin's figure well. However, I have not yet detected a specimen with an intact operculum. There is a lot from the Riu Kiu Islands in the Stanford University collection that has a conic,

reddish operculum. The coiling resembles Daudin's figure, but the shells are sculptured spirally, not transversely. PRAESHAD & RAO in 1933 had an excellent description of *Vermetus (Spiroglyphus) andamanicus*, a vermetid that burrows in the surface of large *Trochus* in the Indian Ocean area. The operculum in this is somewhat but not markedly convex.

Mörch's discussion implied (although he did not actually state) that Daudin described and figured an operculum. What Mörch took to be a basic pattern for the genus was what he had observed in one Caribbean form. As MORTON (1965: 627) has shown, however, there are at least six fairly consistent opercular patterns in the entrenching vermetids. No worker, at present, is ready to split the group into this many subgroups, but establishing for each species which pattern the operculum takes is important for future reference. Before any further splitting is done, we need more work on local populations in areas of abundance to assure that groupings made on the basis of hard-part morphology (shell and operculum) are consonant with what can be observed as to the soft parts, growth habits, reproduction, etc.

Trying to be impartial on the matter of *Spiroglyphus*, both Dr. Michael Hadfield – specialist on Pacific Vermetidae – and I have been keeping watch for specimens that might qualify for designation as neotypes. We have not yet found one that meets all requirements. Nor have we found a satisfactory replacement specimen for *Stoa*.

An alternative to designating fresh material as replacement would be to designate the holotype of some already satisfactorily documented species as neotype of the cryptic taxon. Skillfully enough done, this might be a way of filling three of the open niches for opercular types. For *Stoa* it might be done by designating the lectotype of *Serpula maxima* Sowerby, 1825 (in the British Museum) as the neotype of one of De Serres' species, preferably *Stoa perforans*, which would then be given status, but only as a junior synonym. However, this would be to disregard basic habits of these mollusks – Sowerby's species is associated with corals or on reef rocks and does not attach to bivalves as *Stoa* does. The name would be salvaged at the expense of consistency. *Spiroglyphus* might be reinstated by designating as neotype the holotype of *Vermetus andamanicus* Prashad & Rao, 1933. This latter is extant and in good condition in the museum of the Zoological Survey of India, as reported recently by the curator, Dr. N. V. Subba Rao (letter dated July, 1979). However, the type specimens for this species are much smaller than what Daudin indicated and not on a fissurellid of any sort. I would feel reluctant to set aside a well-proposed name such as this in order to validate an equivocal earlier one. Thus, I would reject the option of

making arbitrary neotype selections. Rather, it seems preferable to jettison both *Spiroglyphus* and *Stoa*.

Declaring *Spiroglyphus* and *Stoa* as *genera dubia* would leave the field open for *Dendropoma*, the first name for entrenching vermetids that was based upon authentic type material. During the last two decades that name has been used in a substantial number of papers (at least 16 titles), not only by malacologists but also by earth scientists and others who are beginning to recognize how useful these mollusks are as markers of shoreline conditions. Living as they do attached to rocks and large shells in the upper intertidal zone, they provide good evidence for any changes in shoreline levels.

Therefore, in view of this practical incentive for nomenclatural stabilization and with the support of Dr. R. Tucker Abbott (personal communication), who on further study has changed his opinion about conserving *Spiroglyphus*, I am asking Dr. Michael Hadfield to join me in a petition to the International Commission on Zoological Nomenclature requesting that *Spiroglyphus* and *Stoa* be suppressed as generic names founded on unidentifiable species.

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NOTES & NEWS

Soviet Contributions to Malacology in 1978

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INTRODUCTION

AS IN PAST YEARS, herein are presented the titles of Soviet malacological literature as abstracted in the Referativny Zhurnal during the year 1978 (see The Veliger 21 (4): 490 for last year's listing and reference to those published earlier). Hopefully, this delineation of mainly Russian contributions to the field of molluscan studies will continue to be useful. Generally, we have followed the editors of the Referativny Zhurnal in the arrangement of categories and often we have appended a short summary of the contents of an individual paper.

To molluscan systematists the most important Soviet work continues to be the often detailed, revisionary monographs which sometimes introduce new taxa and frequently suggest fundamental alterations in accepted systems of classification. Special attention, thus, should be called to:

1) Shileiko's study on the naticoid gastropods as well as his major treatise on the helicacean stylommatophorans of the USSR and to his series of papers on the type species of the genera of the orthurethrous pulmonate family Buliminidae (= Enidae), which introduces a classificatory scheme quite different from that of Zilch; 2) Moskalov's revision of lepidid prosobranchs in which new genera are established and those previously poorly known given more extensive coverage; 3) Ivanova's monograph on the anomalodesmacean verticordiid bivalve *Policordia*; 4) Kudinskaya's and Minichev's description of a new species of the acochlidiid opisthobranch *Hedylopsis* along with a key to all known species;

5) Nesis' review of the enoploteuthid cephalopod subfamily Ancistrocheirinae; and 6) Nigmatullin's review of the systematics of the ommastrephid squids which might be compared to the recently published American work of Wormuth (1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. Bull. Scripps Inst. Oceanogr. vol. 23).

Several notable items dealt with specific geographical areas or faunas: 1) Golikov and Kusakin published a detailed important work on the shell-bearing littoral snails of the USSR; 2) Golikov and Gul'bin extensively treated the prosobranchs of the Kurile Islands, and 3) Gul'bin and Fedchina discussed the closely juxtaposed sublittoral gastropods of the Commander Islands.

Other noteworthy contributions included: 1) Goruchev's discussion of the evolution of the buccinoid gastropod *Neptunea* in the Bering Sea which might well augment the recent research of Nelson (1978. The Veliger 21 (2): 203-215); 2) Nesis and Shevtsov's citation of the first data on the abyssal cephalopods in the Sea of Okhotsk; and 3) Golikov's description of the new genus *Costaria*, the northernmost fascioliid.

Several of the physiological and biochemical papers indicated an intense interest in electrophoretic techniques, especially in distinguishing species. Different authors pointed out that previously recognized forms or 'species' were in reality only variants of single species and thus to be accorded the oblivion of synonymy.

One item which should be of especial interest to American workers doing research on the marine fauna of the north Pacific, north Atlantic or Arctic Oceans was Kafanov's discussion on the evolution of the malacofauna of the north temperate-boreal zones, for which we include a more extensive abstract than usual.

We thank Dr. Joseph Rosewater of the Smithsonian Institution who aided us in obtaining copies of the Referativny Zhurnal from the Library of Congress. Mrs. Mary Jo Dent carefully typed the manuscript.

Abbreviations and acronyms we have used are:

- AN - Akademiya nauk (Academy of Science)
- Biol. Morya - Biologiya Morya (Marine Biology)
- ES - English summary
- Mekh. - Mekhanizmy adaptatsii zhivyykh organizmov k vliyaniyu faktorov sredy (Adaptive mechanisms of living organisms to environmental factors), Leningrad
- NDVS - Nauch. Dokl. Vyssh. Shkol. Biol. Nauk. (Scientific Reports of the Higher Educational School for Biological Sciences)

- SID** – Sbornik Rabot Instituta biologiya morya Dal'nevost. nauch. tsentr. Akad. Nauk. SSSR. – (Papers of the Marine Biological Institute of the Far Eastern Scientific Center, Academy of Science, USSR).
- Vlad.** – Perv. Vses. konf. po mor. biol., Vladivostok. Tezisy dokl. (The first All-Union conference on marine biology, Vladivostok, Thesis Reports)
- VNK** – Vses. nauch. konf. po ispol'z promyslov bespozvonochn. na pishchev. kormov. i tekhn. tseli, Odessa, Tezisy dokl. (All-Union scientific conference for the commercial use of invertebrates for food, fodder and technical purposes, Odessa, Thesis Reports)
- ZEBP** – Zhurnal Evolyutsionnoi biokhimii i fiziologii. (Journal of evolutionary biochemistry and physiology).
- ZZ** – Zoologicheskii Zhurnal (Zoological Journal)

GENERAL

BERGER, V. YA.

1977. The functional organization of the system of salt water adaptations in euryhaline marine mollusks. Vlad.: 15 - 16

BERZHBINSKAYA, N. A.

1977. The regulation of glycolysis at the systemic and molecular levels in molluscan tissues. Vlad.: 26 - 27

[Enzymes involved in glycolysis in chitons, bivalves, gastropods and cephalopods were investigated]

GORBATENKO, S. A., S. D. NIKOLAEV & S. V. POPOV

1975. Factors which influence the isotonic oxygen-carbonate composition of the shells in Caspian mollusks. SID, no. 4: 159 - 166

[Analysis shows that molluscan shells grow in isotopic equilibrium with the ^{18}O content of the water of the Caspian Sea, virtually independent of variations in temperature, suggesting the suitability of paleoisotopic studies of Pontic Pliocene-Quaternary mollusks]

IGNAT'EV, A. V. & G. A. YEVSEEV

1977. The temperature of growth of marine mollusks and their geographical distribution. Vlad.: 57 - 58

[18 species of stenohaline bivalves from the shelf zone of the Sea of Japan and the Sea of Okhotsk were studied; correlations were noted between the geographic distribution of each species and limiting thermal factors]

KAFANOV, A. I.

1978. On the centers of origin and several characteristics of the ecological evolution of the cold and temperate water marine malacofauna of the northern hemisphere. Biol. Morya, No. 1: 3 - 9

[The development of modern northern coldwater marine malacofaunas is intimately related to 3 main Paleogene zoogeographic regions: Northern-Japanese-Sakhalin, Western North American (Columbian) and Boreal-Central Tethyan (northeastern Atlantic), all genetically derived from a more remote tropical source fauna, that of the extremely rich, highly endemic Tethys of the Mesozoic. In the Cenozoic, there were 3 isolated tropical faunas; Indo-West

Pacific, Central American and West Indo-African as well as a small subtropical unit – the Lusitanian-Mediterranean.

The source fauna of the cold-temperate boreal was largely the northern periphery of the tropical areas, especially Tethyan relicts in the North Pacific (Northern Japanese-Sakhalin) derived from the Indo-Malayan Region. Today, the number of North Pacific endemic species is 6 to 8 times greater than in the North Atlantic (Boreal-Central Tethyan). This faunistic evolution, with the concomitant development of strong climatic provincialism, began with the global decline in temperatures in the Cenozoic and the extinction or southward displacement of less adjustable elements. With less competition, survivors in the northern extremes radiated polytypically, forming new but closely related taxa, usually with broad ecological tolerances or eurytopy and dispersed widely through the Boreal and Arctic regions. These elements were unable to reinvade the tropics or subtropics with their high species diversity and filled niches.]

KARPEVICH, A. F. & A. T. SHURIN

1977. The role of manganese in the metabolic processes of Baltic Sea mollusks. Biol. Morya, No. 6: 50 - 57 (ES)

[Increasing concentrations of manganese found in tissues of 3 species of bivalves (*Macoma balthica*, *Mya arenaria*, and *Dreissena polymorpha*) as ambient levels of Mn were raised until, beyond 20 mg/L, death ensued. Shells in Mn solutions for 2 months became blackened as a result of accretion of granules of Mn, and the authors suggest that this may be one manner in which Mn concretions are formed]

KHOKHUTKIN, I. M. & A. I. LAZAREVA

1977. Adaptive polymorphism in populations of terrestrial mollusks. Mekh., p. 151

LUKANIN, V. V.

1977. The complex effects of temperature and salinity on the adaptive reactions of some White Sea mollusks. Mekh., p. 84

REZNIK, Z. V.

1977. Zoogeographical features of the terrestrial molluscan fauna of the Stavropol Heights. Fauna Stavropol', No. 2: 37 - 43

[75 species were found, 42 from the Mediterranean subregion (of which 5 are found in the hilly regions of Europe, 12 from the Mediterranean and Pontic subregions, and 25 Caucasian endemics); 13 species from the Europe-Siberian subregion, and 19 species of wide Palearctic distribution]

ZOLOTAREV, V. N.

1975. Molluscan shell structure and paleotemperature analysis. SID, no. 4: 114 - 158

[Careful analysis of shell structures offers the possibility of evaluating ambient environmental temperatures prevalent at the time of the formation of various parts of the shell]

ZOLOTAREV, V. N. & A. V. IGNAT'EV

1977. Seasonal changes in basic shell layer thickness and the temperature at time of growth in marine mollusks. Biol. Morya, No. 5: 40 - 47 (ES)

[Mass-spectrometric analysis of isotopic-oxygen in the shell structure of 5 species showed correlation with growth intervals and temperature at time of growth. Annulations in the shell usually indicate

reduced shell deposition during the winter at minimal temperatures]

GASTROPODA, GENERAL

ALYAKRINSKAYA, I. O.

1978. Sexual dimorphism and age differences in morpho-biochemical characteristics of some gastropods. *ZZ* 57 (3): 359-363 (ES)

[In some gastropods sexual dimorphism is externally apparent in the different coloration or shape of male and female individuals. However, it is expressed also in lesser known internal ways: in different concentrations of respiratory pigments, total proteins, myoglobin and the specific weight of the hemolymph]

GOLIKOV, A. N. & O. G. KUSAKIN

1978. The shell-bearing littoral gastropods of the USSR. Nauka, Leningrad. 292 pp.; illust.

[This useful handbook discusses 148 species placed in 70 genera, 41 families, 14 orders and 5 subclasses]

GUL'BIN, V. V. & I. YU. FEDCHINA

1977. Sublittoral prosobranch gastropods of the Commander Islands. Vlad., p. 41

[A biogeographical characterization, including data on vertical distribution, is given for the 88 species of prosobranchs occurring around the Commander Islands]

PROSOBRANCHIA

ALYAKRINSKAYA, I. O. & S. N. DOLGOVA

1977. Quantitative contents of the respiratory pigments of *Rapana thomasi* Crosse in the Black Sea. *Dokl. AN SSSR* 236 (6): 1500-1502

[The mg per g of body weight is given for the respiratory substances, hemocyanin, tissue hemoglobin and myoglobin]

GOLIKOV, A. N.

1977. On the family Fascioliidae in temperate waters. *Issled. fauny moryei*, 21/29: 102-104 (ES)

[*Costaria borealis*, n. g., n. sp. was taken at 414 m to the east of Iturup Island in the Kurils, a first record of a fascioliid discovered in the temperate waters of the northern hemisphere]

GOLIKOV, A. N. & V. V. GUL'BIN

1977. Prosobranchs of the Kuril Island shelf. II. Order Hamiglossa-Homoestrophia. [In] Fauna pribrezhn. zon. Kuril. ostrovov (Fauna of the littoral zone of the Kuril Islands), Moscow, pp. 172-268

[Of 241 species and subspecies of prosobranchs, 128 were noted in the orders Hamiglossa, Toxoglossa, Heterostrophia, Ptenoglossa and Homoestrophia. Species of *Mohnia*, *Sipho*, *Aulacofusus*, *Sulcosinus*, *Retifusus*, *Buccinum* (including 2 new buccinid genera), *Trophonopsis*, and *Oenopota* are delineated. The fauna of the southern part of the islands belongs to the Pacific-boreal subregion and differs

from the northern Kuril Islands; a special Kuril subprovince is recognized, especially in the central islands]

1978. Prosobranchs of the Kuril Island Shelf. I. Order Docoglossa-Entomostoma. *Zhivotn. i rastitel'n mir shel'fovikh zon Kurilsk. Ostrovov* (Fauna and flora of the Kuril Island shelf zone), Moscow, pp. 159-223

[Of 241 species and subspecies of prosobranchs collected, 113 belonged to the orders Docoglossa, Fissobranchia, Anisobranchia, Protopoda, Discopoda, Canalifera, Echinospirida, Aspidofora, and Entomostoma. 22 species and subspecies belong to *Puncturella*, *Scissurella*, *Margarites*, *Homalopoma*, *Lacunitunica*, *Onoba*, *Rissoella*, *Trichotropis*, *Torelia*, *Cerithiopsis* and *Furukawaia*. One new genus of Lacunidae and a new subgenus of Trochidae are proposed. Egg capsules of *Capulus nobilis*, *Lunatia pila*, and *Cryptonatica janthostoma* are described and figured for the first time]

GORUCHEV, V. N.

1978. The gastropod genus *Neptunea* Röding in the Bering Sea. Nauka, Moscow, 90 pp.

[Data on the biology, relationships and distribution of the species of *Neptunea* in this area augment a new taxonomic treatment of the genus]

IL'INA, L. B.

1975. On the growth changes of *Arcularia gibbosula*. *SID*, No. 4: 167-173

[A study of the successive growth changes from immature to mature stages in the nassid gastropod *Arcularia gibbosula* clearly indicates the systematic relationships of the species]

KARABELI, O. Z. & B. M. LOGVINENKO

1977. The distribution of the genus *Turricaspia*, section *Laevicaspia*, in the Caspian Sea. *Vestn. Moscow State University, Biologia*, No. 3: 57-63

[On the basis of benthic sampling in the central and southern parts of the Caspian (321 stations), the vertical and horizontal ranges and substrate preferences of the 4 species of *Laevicaspia* were established]

1978. The distribution of *Theodoxus*, family Neritidae, in central and southern parts of the Caspian Sea. *NDVS*, No. 2: 42-46

[321 bottom stations were investigated and the ranges of *Theodoxus* established along with its depth distribution and substrate preferences]

KARTAVTSEV, YU. F.

1976. Color polymorphism in the shells of the gastropod mollusk, *Littorina brevicula* (Philippi). *SID* No. 5: 93-98

[3 color forms of this species occur in Vostok Bay of the Maritime Province]

MOSKALEV, L. I.

1977. Revision of Lepetidae of the World Ocean. *Tr. In-ta okeanol. AN SSSR* 108: 52-78 (ES)

[Two new genera, *Limalepeta* and *Bathylepeta* are established and diagnoses and further information given on *Lepeta*, *Iothia*, *Propilidium*, *Cryptobranchia*, *Notocrater*, *Maoricrater* and *Punctolepeta*]

SHILEIKO, A. A.

1977. Material on the morphology of the Naticoidea and problems of the taxonomy of the superfamily. Tr. In-ta okeanol. AN SSSR 108: 79-97, 9 figs. (ES)

[17 representatives of the superfamily were studied and the families Polinicipidae and Naticidae, with Naticinae and Sininae, recognized. The Polinicipidae are distinguished by having: 1) the cephalopodial portion of the male gonoduct as an open groove; 2) a simple, uniform penis and 3) a horny operculum. The Naticidae have a closed male gonoduct, a variable, complicated penis and a corneous or calcareous operculum; the Sininae have the shell reduced. The new genus *Scarlatia* (type-species, *Natica fortunei* Reeve) is described]

SHUSTOV, A. I.

1978. An analysis of the correlative structures of morphological features of the *Bithynia leachi* group. Zhiznen tsikly, ekol. i morfol. gel'mintov zhivotnikh Kazakhstana (The life cycles, ecology and morphology of helminths of Kazakhstan), Alma-Ata, pp. 52-61

[The conchological features of the *Bithynia leachi* complex were studied statistically, showing that *B. l. troscheli* and *B. l. inflata* are mere varieties and not real subspecies]

OPISTHOBRANCHIA

KUDINSKAYA, E. V. & YU. S. MINICHEV

1977. Psammological Essays. 1. The organization and systematic placement of *Hedylopsis murmanica* sp. n. (Acochlididae). Trudy Petergof. biol. in-ta LGU (Leningrad State University), No. 6: 69-86 (ES)

[The new species is an interstitial opisthobranch. A key to all species of *Hedylopsis* as well as a discussion of the phylogenetic relationships of the Acochlididae are provided]

OBUKHOVA, E. V.

1978. The functional morphology of the epithelium of the digestive glands in the nudibranch *Coryphella rufibranchialis*. Trudy Petrogof. biol. in-ta LGU (Leningrad State University), No. 26: 118-131 (ES)

[A light-optical and ultrastructural examination reveal 3 types of cells: 1) non-differentiated cells, 2) calcium (lime) cells with an albumen-synthesizing apparatus for active ion transport, 3) digestive cells, the cytoplasm of which is filled with heteromorphological vacuoles depending on the stage of the digestive cycle]

TERRESTRIAL PULMONATA

ALYAKRINSKAYA, I. O.

1977. Seasonal variations in the buffering capacity of the hemo-

lymph in *Helix pomatia*. Dokl. AN SSSR 236 (5): 1264-1266

[In periods of summer aestivation, winter hibernation, and nest digging, when normal aerobic respiration is disturbed, there is an increase in the buffering capacity of hemolymph]

MATEKIN, P. V. & V. M. MAKEEVA

1977. Polymorphic esterases and the distribution of *Bradybaena fruticum* Müll. Zh. obshch. biol. 38 (6): 908-913 (ES)

[Electrophoretic analysis of esterases in 3 populations of *Bradybaena fruticum* near Moscow showed that the populations are genetically distinct; esterase polymorphism was also correlated with phenotypic characters such as shell-banding]

SHILEIKO, A. A.

1977. The structure and systematic relationships of the species of the genus *Siraphorus* Lindholm 1925 (Enidae). NDVS, No. 9: 40-46

[Previously 2 species were assigned to *Siraphorus*: *entoptyx* Lindholm, now recognized as the sole species in *Siraphorus*, which is herein accorded subgeneric rank in *Pseudonapaeus*; and *moltschanovi* Likharev and Rammel'meyer, for which a new and separate genus is erected, *Sirapharoides*. The structure of the reproductive organs of Central Asiatic enids differs from those of the Caucasus, and the generic name *Jaminia* is improperly applied to enids from Central Asia, especially the region of Tyan-Shan]

1978. A study of type-species of certain generic taxa in the Buliminidae (=Enidae). 1. Species of Middle and Central Asia. ZZ 57 (3): 344-358 (ES)

[The external appearance and internal reproductive structures of 12 taxa are described: *Pupinidius*, *Serina*, *Subzebrinus*, *Styloptychus*, *Chondrulopsina*, *Mastoides*, *Parachondrula*, *Laeonapaeus*, *Pseudopetraeus*, *Laevozebrinus*, *Chondrulopsis*, and *Pseudonapaeus*]

1978. A study of the type-species of the generic group taxa of the Buliminidae (=Enidae). II. Species of Europe, Near East and Asia Minor. ZZ 57 (4): 512-522 (ES)

[The genital anatomy and shells are described and figured for 10 taxa: *Ena*, *Zebrina*, *Buliminus*, *Pene*, *Jaminia*, *Antichondrus*, *Chondrula*, *Eubrephulus*, *Geminula*, and *Pseudochondrula*]

1978. A study of the type-species of the generic group taxa of the Buliminidae (=Enidae). III. Species of the Crimea and Caucasus. Problems of familial systematics. ZZ 57 (6): 834-850 (ES)

[The groups, *Caucasicola*, *Peristoma*, *Thoanteus*, *Brephulopsis*, *Ramusculus*, and *Retowskia* are characterized by their conchological and reproductive features. A new classification and phylogeny of the family is proposed wherein 8 subfamilies are recognized: Chondrulinae, Eninae, Retowskiinae, Multidentulinae, Bulimininae, Jamininae, Chondrulopsinae and Pseudonapaeinae]

1978. Terrestrial mollusks of the superfamily Helicoidea. Fauna of the USSR, Mollusks vol. 3, prt. 6, 384 pp.; 6 figs. Nauka, Leningrad

[This important revision of the superfamily, with lengthy introduction on the biology and morphology of helicacean snails, discusses 166 Recent and 15 fossil Soviet species, giving figures of the shells and genital anatomy; several alterations of previously accepted suprageneric classifications are introduced]

AQUATIC PULMONATA

GOROKHOV, V. V.

1978. The ecological adaptation of *Lymnaea truncula* to man-made alterations to its normal habitat. Rastitel'n. i zhivotn. naselenie Moskvy i Podmoskov'ya (Floral and faunal populations in Moscow and vicinity), Moscow, pp. 126 - 127

[An account of the occurrence of populations of this species in disturbed environments in the vicinity of Moscow]

KAMARDIN, N. N. & V. A. SOKOLOV

1977. A study of the structure and functional characteristics of the osphradium of *Lymnaea*. Mekhan. sensor. retseptsi (The mechanism of sensory receptivity), Leningrad, pp. 183 - 188

POTANINA, N. V., V. I. STAROSTIN & M. A. LANGE

1977. Autoradiographic examination of amoebocytes in the blood of *Lymnaea stagnalis*. Zh. obshch. biol. 38 (6): 940 - 944 (ES)

SOKOLOV, V. A. & N. N. KAMARDIN

1977. On the possibility of the differentiation of osmotic and chemical components during irritation of the osphradial system of the pond snail. Mekh., pp. 127 - 128

ZAITSOVA, O. V.

1978. Histochemical examination of the osphradium in *Lymnaea stagnalis*. Morfol. osnovy funkts. evolutsii (Morphological survey of functional evolution), Leningrad, pp. 18 - 23

[The osphradium, a chemoreceptor, is an isolated epithelial channel innervated by numerous sensory fibers having their endings on the epithelial surface. Cytochemical study reveals 2 moieties in the epithelial mucus, an acid mucopolysaccharide and a glycoprotein]

ZAITSOVA, O. V., V. A. KOVALEV & L. S. BOCHAROVA

1978. A study of the morpho-functional interrelationships of the sensory epithelium and statoconia in the statocysts of *Lymnaea stagnalis*. ZEBP 14 (3): 307 - 309

[The statoconia have an egg-like shape (from 4.5×2.4 to $11.0 \times 6.6 \mu\text{m}$) and lie freely in the statocyst cavity, in contact with the cilia of the sensitive cells. These cilia are about $7.5 \mu\text{m}$ long and are placed about 1.4 to $1.5 \mu\text{m}$ apart, with supporting microvillary structures scattered among them. The position of the animal is monitored by the constant functional polarization of the sensitivity of the statocysts via the presence or absence of contact between the statoconia and the cilia]

BIVALVIA

ALYAKRINSKAYA, I. O.

1978. Biochemical adaptation to desiccating conditions in bivalves of Kurshsky (Courland) Bay in the Baltic Sea. ZZ 57 (1): 136 - 138 (ES)

[During desiccation, calcium ions, provided by the dissolution of the crystalline style and the shell itself, are incorporated as buffers into the hemolymph to offset increased acidity in *Anodonta complanata*, *Unio tumidus*, and *Dreissena polymorpha*]

BUROVINA, I. V., O. A. GONCHAREVSKAYA & N. B. PIVOVAROVA

1978. X-ray microanalysis of the elementary composition of hemolymph in the mussel, *Mytilus edulis*. ZEBP 14 (3): 241 - 245

[In a study of the ions of Na, K, Cl, Ca, P, S, and Mg, in mussels in waters of low salinity, it was shown that K was accumulated in the hemolymph at higher concentrations than that of the environmental medium]

GOROMOSOVA, S. A.

1977. Elements of carbohydrate metabolism of mussel (*Mytilus*) in connection with adaptations to environmental extremes. Ekol.-fiziol. issled. v prirode i eksperiment. Frunze, pp. 155 - 169

IVANOVA, V. L.

1977. New data on the composition and distribution of the deepwater genus *Policordia* Dall, Bartsch, and Rehder. Tr. Inta okeanol. AN SSSR 108: 173 - 197; 18 figs. (ES)

[2 new subgenera with 8 new species are recognized anatomically: *Angustebranchia* with 5 species in the ultra-abyssal Kurile-Kamchatka Trench and *Latebranchia* with 8 species, mostly of bathyal-abyssal occurrence in the Pacific Ocean]

KARPENKO, A. A.

1977. Cardiac rhythm and the physiological condition of the littoral scallop (*Patinopecten yessoensis*). Vlad.: 65 - 66

[Cardiac rhythm is a good indication of the level of activity of metabolism in bivalves. In this scallop, it rises with rising temperatures, increases after swimming and in the proximity of predators like starfish, and rises sharply with lowered salinity]

KARTAVTSEV, YU. F., S. M. NIKIFOROV & A. I. PUDOVKIN

1977. The taxonomic position and genetic variability of *Crenomytilus grayanus*. VNK, pp. 41 - 42

[Electrophoretic analysis fails to support the contention of Smirnov that there are 2 taxonomically separable forms of this species]

KHOBOT'EV, V. G.

1978. On the ability of unionids to regulate the ionic composition of water. Biopovrezhdeniya materialov i zashchita ot nich (Bio-damages of materials and the defense against them), Moscow, p. 11

[Freshwater bivalves are indicators and regulators of alkaline concentrations]

KRASNOV, YE. V.

1977. Non-specific adaptation by marine mollusks to the process of calcification. *Materiali 2-go Simpoz. Protsesti adaptatsii i biol. aktivn. veshchestv*, Vladivostok, 1975, pp. 42 - 46

KUKIN, A. F.

1976. The reproductive cycle of *Swiftopecten swifti*. *SID No. 5*: 122 - 130

[Normally gonochoristic (only 1 hermaphrodite found in more than 200 individuals), *Swiftopecten swifti* in Vostok Bay spawns from August through the first half of September at 21-22° C. Histological studies document changes in the gonad]

LOGVINENKO, B. M., O. P. KODOLOVA & O. YU. PRABDUKHINA

1979. *Redkollegiya Biol. Nauki* (Editorial Board, Biological Science), Moscow, 17 pp. (manuscript deposited in VINITI)

[Electrophoretic analysis of populations of *Mytilus galloprovincialis* and *Ostrea edulis* in the Black Sea]

LYUTSKANOV, D.

- 1975 (1976). A biometrical study of *Dreissena polymorpha* Pallas in Shablessky Lake. *Nauch. trudy Plovdiv. Univ., Biol.* 13 (4): 227 - 236 (Bulgarian; Russian and French summaries)

[Analysis of 2 populations from 2 depths showed adaptive differences in both conchological and anatomical parameters]

MARCHENKO, A. A. & A. L. POLENOV

1977. On the participation of Gomori-positive neuro-secretory cells in *Mytilus edulis* L. in adapting to hypoxia. *Ekol.-fiziol. issled. v prirode i eksperimente*. Frunze, pp. 223 - 224

MARGULIS, B. A. & G. P. PINAEV

1977. The composition of the muscle albumens and its systematic significance in bivalve classifications. *Vlad.*: 99

[Adductor muscle extracts from 25 species of bivalves from the Seas of Japan and Okhotsk were examined electrophoretically and a phenogram of relationships constructed, which validated the classification of Nevesskaya and her colleagues]

MEDVEDEVA, L. A.

1976. The reproductive cycle of *Spisula sachalinensis*. *SID No. 5*: 131 - 135

NEVESSKAYA, L. A.

1975. Ontogenetic development of the shell and various modes of speciation in bivalves. *SID No. 4*: 17 - 34

[Analysis of ontogenesis of the shells of 30 Miocene and Quaternary species of bivalves revealed the occurrence of the evolution of some species by neotony]

NIKIFOROV, S. M.

1977. On the systematics of the oysters of the southern littoral of the maritime province. *Vlad.*: 108

[Electrophoretic analysis of various tissue extracts shows that *Crassostrea gigas* is a single species, not 3 distinct ones]

NIKIFOROV, S. M. & A. I. PUDOVKIN

1977. Genetic and morphometric variability in *Crassostrea gigas*. *VNK*: 60 - 61

[Electrophoretic data indicate that only a single species of oyster, *Crassostrea gigas*, inhabits Peter the Great Bay]

NISTRATOVA, S. N., V. N. DANILOVA & I. S. NIKOL'SKAYA

1978. Seasonal changes in the sensitivity to acetylcholine in the cardiac muscle of *Anodonta complanata* and *A. piscinalis*. *ZE BP* 14 (4): 358 - 364 (ES)

[The greatest change in sensitivity occurs at spawning when gametes are transferred and fertilization takes place with retention of zygotes in the ctenidia and before development of the glochidia in the marsupium]

PINAEV, G. P.

1978. Levels of organization in the retractive apparatus of the adductor muscles of bivalves. 3-ya vsyes. konf. po biokhimi myshch (Third All-Union conference on the biochemistry of muscles), Moscow, pp. 13 - 15

[Electrophoresis of muscle proteins in 26 species of bivalves confirmed their systematic placements and established a correlation between the contractile system and the quantities of actin, myosin and paramyosin]

PLISETSKAYA, E. M.

1977. Insulin in mollusks and its role in the regulation of the carbohydrate metabolism. *ZEBP* 13 (5): 600 - 606 (ES)

[Insulin or an enzyme very similar to it is produced in intestinal cells of the freshwater mussels *Anodonta cygnea* and *Unio pictorum*]

PREMINGER, N. K.

1977. Protein composition of the contractile apparatus of muscle tissue in the mussel, *Crenomytilus grayanus*. *Biol. Morya*, No. 5: 82 - 84

[Electrophoretic analysis showed high paramyosin and low myosin in anterior byssal retractor muscle and 2 parts of the adductor muscles, but the reverse obtained in muscle tissues of the mantle, heart and foot]

PUNIN, M. YU.

1978. The cellular composition of the digestive gland of White Sea lamellibranchs. *Trudy Petergof. biol. in-ta LGU* (Leningrad State University), No. 26: 132 - 144 (ES)

[Morphological and histological studies were undertaken on *Mya arenaria*, *M. truncata*, *Cyprina islandica*, *Cardium ciliatum*, *Serripes gronlandicus*, *Musculus discors* and *Modiolus modiolus*. A great deal of similarity was discovered in the histological structure of their digestive glands]

ROMANENKO, V. D., O. M. ARSAN, V. D. SOLOMATINA,

S. P. VESEL'SKII, V. P. PRYADKO & N. YU. YEVTUSHENKO

1977. Ionic exchange and the role of calcium in *Anodonta cygnea*. *Gidrobiol. zh.* 13 (5): 115 - 119

SKUL'SKII, I. A., N. B. PRIVOVAROVA, T. I. IVANOVA, V. G. LEONT'EV, I. V. BUROVINA & A. F. FEDOROV

1977. The adaptation of neuro-muscular cells in mussels to decreases in salinity. *Vlad.*: 129 - 130

STADNICHENKO, A. P.

1978. Mollusks of the family Sphaeriidae in the Crimea. Report I. Vestn. zoologii 1: 67-73

[4 species were found in 40 stations from Simferopol to Feodosia: *Euglesa casertana*, *E. personata*, *Musculium lacustre* v. *major*, and *E. henslowana* v. *inappendiculata*, the last being new to the Crimea. The first 3 are rheophilic while the last prefers slow water and is found only in Salgira Creek at Pereval'noye]

SVESHNIKOV, V. A.

1977. Aspects of the life cycle of the Far Eastern mytilid species *Crenomytilus grayana*. Dokl. AN SSSR 226 (4): 1028-1031

[Interacting periods of the life cycle may be recognized: The pelagic larvae are attracted to the benthic adults, settle and attach selectively by their byssal threads; initially the immatures live in the lower tier, sheltered somewhat from predators and grow rapidly; subsequently growth is hindered as competition increases for space and resources]

VARAKSYN, A. A.

1977. On the neurosecretions of the mytilid (*Crenomytilus grayanus*) and the pectinid (*Patinopecten yessoensis*). Biol. Morya. No. 4: 58-65 (ES)

[Morphometric and cytological investigations show that neurosecretory activity in the cerebropleural, visceral and pedal ganglia of the males and females of this species alters during the course of the year, presumably reflecting a correlation with sexual activity]

VASIL'EVA, V. S.

1978. Heat retention of cells in the upper littoral sand dwelling infaunal bivalves of Peter the Great Bay (Sea of Japan). Biol. Morya. No. 1: 53-57

[8 species are dealt with. Heat retention in these bottom dwelling, infaunal invertebrates depends on their vertical and geographical distribution as well as on the ambient temperature]

YAKOVLEV, YU. M.

1978. The reproductive cycle of the giant oyster (*Crassostrea gigas*) in the Sea of Japan. Biol. Morya, No. 3: 85-87 (ES)

[Histological study of gametogenesis shows, during the course of the year, specific seasonal stages in the gonad: spawning, post-spawning, reduction, growth, maturation and prespawning]

YAVNOV, S. V.

1977. Secretion of growth layers in the internal structure of the shell in some species of the Mactridae. Vlad.: 156-157

[*Spisula sachalinensis*, *S. voyi*, and *Mactra sulcalaria* were studied; the outer shell layer is cross-lamellar and has 2 sublayers; the inner shell layer is complex-cross-lamellar; growth intervals, for as short a time as a week, can be detected]

YEVSEEV, G. A.

1975. Characteristics of the ontogenesis of the pallial sinus in *Macoma balthica*. SID, No. 4: 75-82

[Slight differences in the configurations of the pallial sinus, apparently correlated with salinity, separate western (Arctic-Baltic) and eastern (Pacific) populations of *Macoma balthica*]

1976. The origin of Vostok (East) Bay in the Sea of Japan and the history of its bivalve fauna. SID, No. 5: 23-62

[The formation of Vostok Bay began 8000-9000 years BP during a cold boreal period when 22 species of bivalves, mostly cold water forms, were found there. Postglacial transgression (8000-2000 years BP) found 45-49 species with the % of cold water species declining. Greatest diversity occurred during the last transgression when the sea level was up to 1 m higher than at present and 60 bivalve species were present, most of them warm water elements]

ZORINA, I. P.

1978. New bivalve species of the Gulf of Tonkin (South China Sea). Tr. zool. inst. AN SSSR 61: 193-203

[From the region of the delta of the Red River, Fai-Tsi-Long Archipelago and Hainan Island are described as new with figures, dimensions, distributional and ecological data: *Phacoides scarlatoi*, *Pillucina vietnamica*, *Codakia golikovi*, *Pitar levis*, *P. sulcata*, *Diplodonta gurjanovae*, *Raeta lactea*, *Moerella fragilis*, and *Gari tonkinensis*]

CEPHALOPODA

BURUKOVSKI, R. N., G. V. ZUEV, CH. M. NIGMATULLIN &

M. A. TSYMBAL

1977. A methodical basis for recognizing the extent of maturity in the female reproductive system of squids, using *Sthenoteuthis pteropus* as an example. ZZ 56 (12): 1781-1791

[Several stages of the continuous process of maturation are recognized and suggested to be typical of all squids. These are separable mainly into those associated with oogenesis along with the development of accessory reproductive organs, and those connected with the accumulation of mature eggs in the oviduct]

DUBININA, T. S.

1977. Characteristics of the morphology of the larvae of Onychoteuthidae in the tropical Atlantic. VNK, pp. 34-35

[The larvae of 4 species are described, falling into 2 types: 1) the more primitive *Onykia* including *Onykia* and *Moroteuthis* with mantle length of 8 mm; and 2) the more advanced *Onychoteuthis*, including *Onychoteuthis* and *Ancistroteuthis* with mantle lengths between 13-15 mm. Allometric growth patterns are noted in the arms, tentacles, and penis]

NESIS, K. N. & G. A. SHEVTSOV

1977. Preliminary information on the abyssal cephalopods in the Sea of Okhotsk. Biol. Morya, No. 5: 76-77 (ES)

[In bottom dredgings of up to 3400 m in June, 1975, 7 specimens of 5 species were taken: *Gonatopsis borealis*, *G. okutani*, *Grimptoteuthis albatrossi*, *Belonella borealis*, *Benthoctopus profundorum*. All specimens, except those of the first species, were mature or maturing, their dimensions close to or exceeding the maximum reported. It was noted that *Belonella pacifica pacifica* is a synonym of *B. belone* and that *B. p. borealis* is an independent species]

NESIS, K. N.

1978. The conference on the study of cephalopods. Kaliningrad, October 1976. Biol. Morya, No. 1: 83-84

[Summary of papers presented at meeting]

1978. The subfamily Ancistrocheirinae (Enoploteuthidae). ZZ 57 (3): 446-450 (ES)

[The subfamily previously included *Thelidioteuthis alessandrinii*, known from a larvae and juvenile, and *Ancistrocheirus lesueuri*, known only from adults. Recently collected specimens show that *Thelidioteuthis* is a junior synonym of *Ancistrocheirus* though both *alessandrinii* and *lesueuri* are good species, the former being cosmopolitan in the tropics; the range of the latter is unknown]

NIGMATULLIN, CH. M.

1977. Relationships and ecological structures in squids of the family Ommastrephidae. VNK, pp. 55-56

[Taxonomic characters grade from most primitive in the subfamily Illicinae, to intermediate in Todarodinae and Ornithoteuthinae to most advanced in Ommastrephinae. Ecological specializations parallel this trend: more primitive representatives are sublittoral, mostly partly benthic forms which lay eggs on the bottom, intermediate forms are found mostly over the slope, and the most advanced, or evolutionarily youngest, include oceanic forms with pelagic eggs and considerable development of photophores]

PETROV, O. A.

1977. On the fertility of the New Zealand squid, *Notodarus sloani sloani*. VNK: 63-64

[The gonads of 40 females, collected in February-April, were examined. 3-4 generations of eggs, from 0.1-1.5 mm in diameter, were discovered in the ovaries in various phases. Most oocytes were on the surface of the ovary, spherical or oval in shape, and from yellowish to amber in color. Although no clear relationship between the size of the female and the diameter of the ova was noted, there was a direct correlation between the size of the female and the number of ova: as the length of the mantle increased to 1 cm, the quantity of eggs grew to an average of 80 000 each; females larger than 38 cm had as many as 550 000]

ROZENGART, E. V., S. P. SHEVTSOVA & L. M. EPSHTEIN

1977. The properties of cholinesterase in the optic ganglia of the Teuthidae [sic]. VNK: 76-77

[A large amount of cholinesterase is contained in the tissues of the optic ganglia, and its properties vary, as a correlate of the life history of the animal, in different species, such as *Ommastrephes bartrami* and *Illex illecebrosus*]

SHEVTSOVA, S. P., A. P. BRESTKIN, K. N. NESIS & E. V. ROZENGART

1977. On the identity of the affinities of cholinesterase in the optic ganglia of *Ommastrephes bartrami* from the South Atlantic and from the Great Australian Bight. Okeanologia 17 (6): 1102-1106

ZALYGALIN, V. P., G. V. ZUEV & CH. M. NIGMATULLIN

1977. Characteristics of spermatophore production and male fertility in *Sthenoteuthis pteropus* (St.). VNK: 37-38

[A close correlation between mantle length and spermatophore length (of spermatophores in the spermatophoric sac) was established in a sample of over 70 male specimens; evidence for size dimorphism in spermatophores in the mantle cavity was presented]

ZUEV, G. V. & CH. M. NIGMATULLIN

1977. Basic elements of the internal structure of *Sthenoteuthis pteropus* (St.) in the northern part of the tropical Atlantic. VNK: 38-40

[Variable dimensions of the mantle are correlated with geographic positions and climatic conditions]

POLYPLACOPHORA

SIRENKO, B. I.

1976. Chitons of East Bay in the Sea of Japan. SID, No. 5: 87-92

[17 species are recognized with the following geographical affinities: 64% low-Boreal, 24% subtropical-low Boreal, and 12% pan-Boreal]

CALIFORNIA

MALACOOZOLOGICAL SOCIETY, Inc.

is a non-profit educational corporation (Articles of Incorporation No. 463 389 were filed January 6, 1964 in the office of the Secretary of State). The Society publishes a scientific quarterly, the VELIGER. Donations to the Society are used to pay a part of the production costs and thus to keep the subscription rate at a minimum. Donors may designate the Fund to which their contribution is to be credited: Operating Fund (available for current production); Savings Fund (available only for specified purposes, such as publication of especially long and significant papers); Endowment Fund (the income from which is available. The principal is irrevocably dedicated to scientific and educational purposes). Unassigned donations will be used according to greatest need.

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Sea Star Predation on Rock-Boring Bivalves

BY

E. C. HADERLIE

Department of Oceanography
Naval Postgraduate School, Monterey, California 93940

THE MONTEREY FORMATION shale which forms extensive outcrops under kelp beds in southern Monterey Bay is penetrated by several species of boring bivalves of the families Mytilidae and Pholadidae. Divers examining these shale outcrops can see the protruding siphons of many of these borers and in some cases can make positive identification of the species by siphon morphology (HADERLIE *et al.*, 1974). Most borers retract the siphons into the burrow when touched and a few can retract the siphons within the shell. None have methods of blocking the burrow entrance once the siphons have been withdrawn.

The sea star *Pisaster brevispinus* (Stimpson, 1857) is a common predator in the shallow subtidal water in Monterey Bay. It is seen on soft bottoms as well as on the exposed shale reefs. On soft bottoms the sea star feeds on a variety of buried bivalves by digging down to them or by extending the central tube feet downward into the sediment for as much as 17 cm and lifting the clams up to the mouth (VAN VELDHIJZEN & PHILLIPS, 1978). On rocky reefs the sea star often is seen over pholad and boring mytilid burrows, and when examined has its stomach everted and pressed into the opening of the burrow.

When large pieces of shale are excavated by divers, or broken free by a heavy dredge, and brought ashore for examination, it is found that at least 50% and sometimes 100% of the bivalve boreholes are empty or contain only the valves of dead borers. Some of these valves are from young immature animals.

Direct evidence of predation by *Pisaster brevispinus* on boring bivalves has been obtained recently. In an attempt to determine the growth rates of boring bivalves, a number of animals in the young, active boring stage have been removed from their natural burrows in shale, identified and measured, then re-introduced into "artificial" burrows drilled into shale similar to that from which the animals came. Species used in these experiments include *Lithophaga plumula* Hanley, 1843; *Adula falcata*

(Gould, 1851); *Chaceia ovoidea* (Gould, 1851); *Neta-stoma rostrata* (Valenciennes, 1846); *Parapholas californica* (Conrad, 1837); *Penitella penita* (Conrad, 1837) and *Penitella gabbi* (Tryon, 1863). The experimental burrows are cylindrical (not the normal pear-shape) and fit the bivalves snugly. The open end of the burrow of each is plugged with a perforated stopper allowing the siphons to extend out into the water but preventing the animal from falling out of the burrow. The panels of shale containing the borers are then put in racks and placed on the bottom in approximately 10 m of water; each month the shale panels are recovered and x-rayed to determine growth rates of the borers. The radiation does not appear to harm the experimental animals for they remain alive and continue to bore at the same rate as control animals. During the past year mortality among all of these experimental animals has been high but the cause was unknown until racks were recovered where several *Pisaster brevispinus* were found on the shale panels in the process of feeding on representatives of all the borers named above. Careful observation revealed how the bivalves were attacked. In some cases the sea star had extended its central tube feet through the hole in the stopper, attached the tube feet to the shell of the borer, then pulled the bivalve up against the stopper until this plug popped out and the borer (and stopper!) could be enveloped by the sea star's stomach. When this tactic failed, presumably because the stopper could not be dislodged, *Pisaster* everted its stomach and inserted it through the hole in the stopper into the burrow. In these cases the stomach did not appear to enfold the borer, but digestive enzymes apparently were secreted over the borer and the bivalve digested in its own burrow. In nature, where the shape of the burrow precludes removal of the animal in one piece, this latter method of feeding is perhaps the one used and would account for the clean, empty shell valves found in many burrows.

The experiments are continuing, but now the shale panels are housed in cages that exclude predatory sea stars.

Literature Cited

- HADERLIE, EUGENE CLINTON, J. C. MELLOR, C. S. MINTER III & G. C. BOOTH
1974. The sublittoral benthic fauna and flora off Del Monte Beach, Monterey, California. *The Veliger* 17 (2): 185-204; 3 pls.; 9 text figs. (1 October 1974)
- VAN VELDHIJZEN, H. D. & D. W. PHILLIPS
1978. Prey capture by *Pisaster brevispinus* (Asteroidea: Echinodermata) on soft substrate. *Mar. Biol.* 48: 89-97

Generous Donation by the Conchological Club of Southern California

On the same day that the January issue was delivered to us by the printer, a very generous contribution to the Veliger Endowment Fund from our friends, the Conchological Club of Southern California, arrived in the mail. We are very grateful for the continued support, which serves a twofold purpose: firstly, it helps us in our effort to keep the cost of the journal at its — in these days of galloping inflation — unusually low price; and secondly, it encourages us in what we hope to be a worthwhile undertaking.

ERRATUM

Mrs. Helen DuShane has informed us that Dr. Joseph Rosewater of the National Museum of Natural History, Washington, D. C., has advised her that the museum number of *Epitonium appressicostatum* is in error. Lines 14 ff. in the second column on p. 107 of volume 22 of our journal should read:

"... 2 specimens, as *Epitonium appressicostatum* (USNM 678703), ..." — not (USNM 59334). Mrs. DuShane regrets the error.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or

by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

REGARDING POSTAL SERVICE

We are much disturbed by the steadily increasing number of premature claims for supposedly "missing" issues of our journal. Since we have announced on numerous occasions that our journal is mailed on the dates printed in the issues, *i. e.*, number 1 on July 1, number 2 on October 1, number 3 on January 1 and number 4 on April 1 of each volume year, it is unreasonable to expect delivery of the issues earlier than at least one week after these dates; however, a much longer time must be allowed for delivery to addresses at various distances from Berkeley. Thus, for example, a two weeks lapse is not unusual for as short distances as 500km; and up to 3 and 4 months must be counted on for addresses in the Far East and in Africa. We are faced with the alternative of not replying to what we must consider premature claims or, if the trend continues, we must increase our subscription rates to cover these additional expenses. Our past efforts at keeping the subscription rate as low as possible are, we believe, sufficient evidence that we simply cannot afford any other course of action. The postal service causes us enough financial losses. Therefore, we urgently request that before a claim is made, the time schedule be carefully checked. We are grateful for the understanding of this difficult situation shown by many librarians and will be grateful to those who, heretofore being perhaps eager to make sure that the library receives what is coming to it, will exercise a little patience.

Claims for defective or missing pages must reach us within 60 days from the publication date. We will not respond to claims for missing issues made less than 30 days by domestic addressees, or less than 60 days by foreign addressees after the publication date of our journal issues.

Your harassed Editor.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the Veliger goes to domestic addresses, and a deposit of US\$18.00 for all foreign addresses (including PUAS).

Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

We have read in January this year that at a meeting of the U. P. U. (Universal Postal Union) the decision was made that all international postage rates will be doubled in 1981; that, however, in view of the very low rates in effect in the U. S. A. (due to the depreciation of the dollar), this country would be allowed to increase its foreign rates in October 1980. We have, however, not been able to get any confirmation from the postal authorities in this area. If it turns out later to be true, we may be forced to ask our members and subscribers in foreign countries for a supplemental payment to cover the increase. This will be especially true in the cases where the journal is being sent by Air Mail.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our re-mailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. The following charges must be made:

change of address - \$1.-

change of address and re-mailing of a returned issue
- \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$15.00 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept

a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

At a Regular Membership meeting of the Society in November 1968 a policy was adopted which, it is hoped, will assist in building up the Endowment Fund of the Society.

An issue of the journal will be designated as a Memorial Issue in honor of a person from whose estate the sum of \$5000.- or more has been paid to the Veliger Endowment Fund. If the bequest is \$25 000.- or more, an entire volume will be dedicated to the memory of the decedent.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of United California Bank in Berkeley, California. This institution has agreed to honor such drafts without charge. UNESCO coupons are **N O T** acceptable except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these char-

ges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper covered and cloth bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644. The same applies to the supplements still in print with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. West at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from Mr. West are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspeidea of California by Prof. R. Beeman,
and The Thecosomata and Gymnosomata of the Cali-
fornia Current by Prof. John A. McGowan]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announce-
ment elsewhere in this issue.

Supplement to Volume 11:

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen
DuShane]

[Growth Rates, Depth Preference and Ecological Succes-
sion of Some Sessile Marine Invertebrates in Monterey
Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement
is exhausted. Copies may be obtained by applying to Dr.
E. C. Haderlie, U. S. Naval Post-Graduate School, Mon-
terey, CA(lifornia) 93940.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

Volume 1: \$1.50	Volume 6: \$4.50
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Supplement to Volume 6: \$1.50; to Volume 18: \$3.00

California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, 792 Laurie Avenue, Santa Clara, CA 95050.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644. Orders should be sent directly to Mr. West.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA(lifornia) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15

but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

OPEN POSITION FOR MALACOLOGIST

FIELD MUSEUM OF NATURAL HISTORY announces a search for an Assistant Curator of Invertebrates in the Department of Zoology. Appointment of the successful candidate, who must have a Ph. D. or substantially completed all degree requirements, will take place about January 1, 1981, for a three year term. Preference will be given to workers on the systematics of freshwater or marine mollusks. Research will be of the candidate's choice, with 50% time available.

Further information can be obtained from: Dr. Robert K. Johnson, Chairman, Invertebrates Search Committee, Division of Fishes, Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago, Illinois 60605, U. S. A. The search will close in September 1980. Field Museum of Natural History is an Equal Opportunity Employer.

IMPORTANT NOTICE

If the address sheet of this issue is PINK, it is to indicate that your dues remittance had not arrived at the time the mailing was prepared (*i. e.*, by March 1, 1980). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc.

by April 15, 1980. However, in view of the unreliability of the postal service, members should not be alarmed by this notice as their remittances may be received between the first of March and the date of mailing this issue on April 1. From overseas addresses we must allow a minimum of 6 weeks for surface mail. On the other hand, it is possible that the envelope and dues notice enclosed between pages 292 and 293 of the January issue have escaped your attention. If so, now is the time to use them to avoid interruption in the delivery of this periodical.

BOOKS, PERIODICALS, PAMPHLETS

Note on a Panamic Province Cone

Two papers in a new conchological publication, *The Shell Collector*, discuss the synonymy of *Conus brunneus* Wood, 1828. Under the title "The *Conus bartschi/brunneus* controversy now over," Alex Kerstitch shows that the two forms are separable and that they occur in slightly different habitats. The spire of *C. bartschi* is smooth, whereas that of *C. brunneus* has 2 to 6 incised grooves. There is also a difference in range, and *C. andrangae* Schwengel, 1955, is shown to be a synonym of *C. bartschi* Hanna and Strong, 1949. A companion note by John K. Tucker in this journal reinforces Kerstitch's view, with further illustrations.

KERSTITCH, ALEX [title cited above]. *The Shell Collector*, no. 2, pp. 38-41; 4 color figures. 1979.

TUCKER, JOHN K. "*Conus bartschi* and *Conus brunneus*: two closely related Eastern Pacific cone shells." *ibid.*, pp. 42-43; 13 figs.

A. Myra Keen

Malacological Review

P. O. Box 420, Whitmore Lake, Michigan 48189, U. S. A.
vol. 12 (1-2), iv + 186 pp.; illust.

As most of its predecessors, this volume contains several original research articles, followed by several "Brief Communications." On pp. 97 - 104 are found announcements

of past and future events of interest to malacologists. And on page 105 starts, "Contents of Current Malacological Periodicals."

Among the research articles, the one by R. I. Johnson, entitled "The types of Unionacea (Mollusca: Bivalvia) in the Museum of Zoology, The University of Michigan," is of special interest to taxonomists dealing with this freshwater group. In the interest of stabilizing taxonomy, the whereabouts of extant type specimens is of singular importance. Many similar lists have been published either for certain groups or for material described by a particular worker.

For reasons this reviewer does not understand, the price of this work to individual subscribers is still only \$10. (\$10.50 for subscribers in all foreign countries).

R. Stohler

A Field Guide to the Land Snails of Britain and North-west Europe

by M. P. KERNEY & R. A. D. CAMERON, illustrated by GORDON RILEY. 288 pp.; 649 illustrations (408 in color on 24 plates); 392 distribution maps. Collins, Publishers, 14 St. James Place, London, SW1A 1PS. £5.50.

7 June 1979

This remarkably well organized, relatively small (pocket size) book is one this reviewer wishes he had had available in his younger days when he was studying Swiss mollusks. Now, some 50+ years later, it is pleasant to renew acquaintance with some "old friends."

The introductory pages, as is not uncommon in books of this type, contain hints on the use of the book, explain the format adopted, discuss biology, habitat and related topics; a brief section deals with collecting and identifying land snails. A glossary of "shell terms" concludes the "preamble."

A systematic check-list of all species treated in this book occupies pages 39 to 47. We are especially pleased that the authors list in this part in what we consider the only fully correct manner; that is, complete with author and year of original description.

As far as memory will serve, the color figures appear true to life. The quality of the line drawings is high. The text is clear and easy to understand. An interesting detail of some of the distributional maps is the indication that the particular species is spreading or receding, as the case may be.

If we give the impression that we like the book — all we have to say is: we do.

R. Stohler

Indexes to the Nautilus

Geographical (Vols. 1-90) and Scientific Names (Vols. 61-90). Edited by R. TUCKER ABBOTT. American Malacologists, Inc., Publ. P. O. Box 2255, Melbourne, Florida 32901. 238 pp.; US\$24.00. (26 October 1979)

The geographical index of the first 90 volumes of the *Nautilus* was compiled by Mrs. Margaret Crockett Teskey, who, for many years, was the Secretary of the American Malacological Union. This index occupies 80 pages. It is arranged alphabetically by country, subdivided, in the case of the United States, by individual States. A further subdividing has been made under each of the categories mentioned into 'Land, Freshwater,' 'Marine' and 'Fossil.' Under these final subheadings, the titles are arranged strictly alphabetically.

The index to the scientific names in the *Nautilus*, compiled by Mrs. Louise Burrell Hastings, occupies the final 158 pages of the volume. It is stated in a sort of Foreword that this index includes 24 000 entries. We did not check the accuracy of this statement! This list is also strictly alphabetical. Each species is listed under its trivial name and also under the genus name.

In sampling the book, we did not detect any obvious typographical errors. But even if there are such errors or possible inadvertent omissions, they will not materially detract from the value of the compilation.

R. Stohler

Pacific Coast Subtidal Marine Invertebrates

by DANIEL W. GOTSHALL & LAURENCE L. LAURENT. Sea Challengers, Los Osos, California 93402. 112 pp.; 160 color illustrations on 40 plates; 2 pp. line drawings; 5 maps. US\$10.87 paperback; \$14.20 hard cover, mailing and handling included. 1979

This book will be welcomed by the diving enthusiasts, who, with the aid of modern SCUBA equipment, can explore the shallower portions of the nearshore waters of the Pacific Coast of North America. This area is still a very rich one, in spite of the seemingly determined efforts of modern man to destroy it. We can think of no more powerful way of convincing people that the conservation and protection of this rather fragile environment is worth every effort than to have as many people as possible visit and study the subtidal area.

Such visits will reveal an unexpected wealth of fascinating and, sometimes, bizarre forms of living beings,

sometimes startlingly colorful and yet, at the same time, often difficult to see because of their cryptic habit.

The well-printed reproductions of masterfully taken color photographs in this book will satisfy the curiosity not only of the novice diver, but also that of a more experienced diver. We must applaud the authors for their choice of "shots" for reproduction, although we think that many users would like to have several dozen other species included. There are "only" 44 molluscan species represented out of a possible 700 or 800 and the especially colorful nudibranchs are represented "only" by 14 species. It must have been a painful job to eliminate dozens and dozens of excellent shots from consideration for inclusion.

R. Stohler

**Cephalopods from Deepwater Dumpsite 106
(Western Atlantic):**

Vertical Distribution and Seasonal Abundance

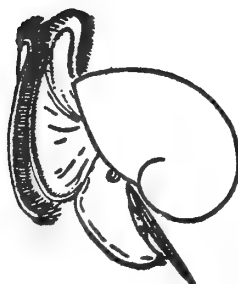
by C. C. LU & CLYDE F. E. ROPER. Smithsonian Contributions to Zoology, No. 288. 36 pp.; 11 text figs.; 5 tables (2 of these in the appendix). 1979

Dumpsite 106 is an area about 160 km east of Cape Henlopen, Delaware. In size it is 20' by 30'. Water depth ranges from 1550 m to 2750 m. "The dumpsite is used for the disposal of acid waste, industrial chemicals and radioactive wastes, . . ."

The objectives of the study were to determine species composition, vertical distribution, seasonal occurrence, relative abundance, spawning tendencies, and relationship to water types of 36 species of cephalopods (octopus and squids).

The results obtained on 4 cruises are detailed in the 2 tables in the appendix, occupying 11 pages.

R. Stohler



THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

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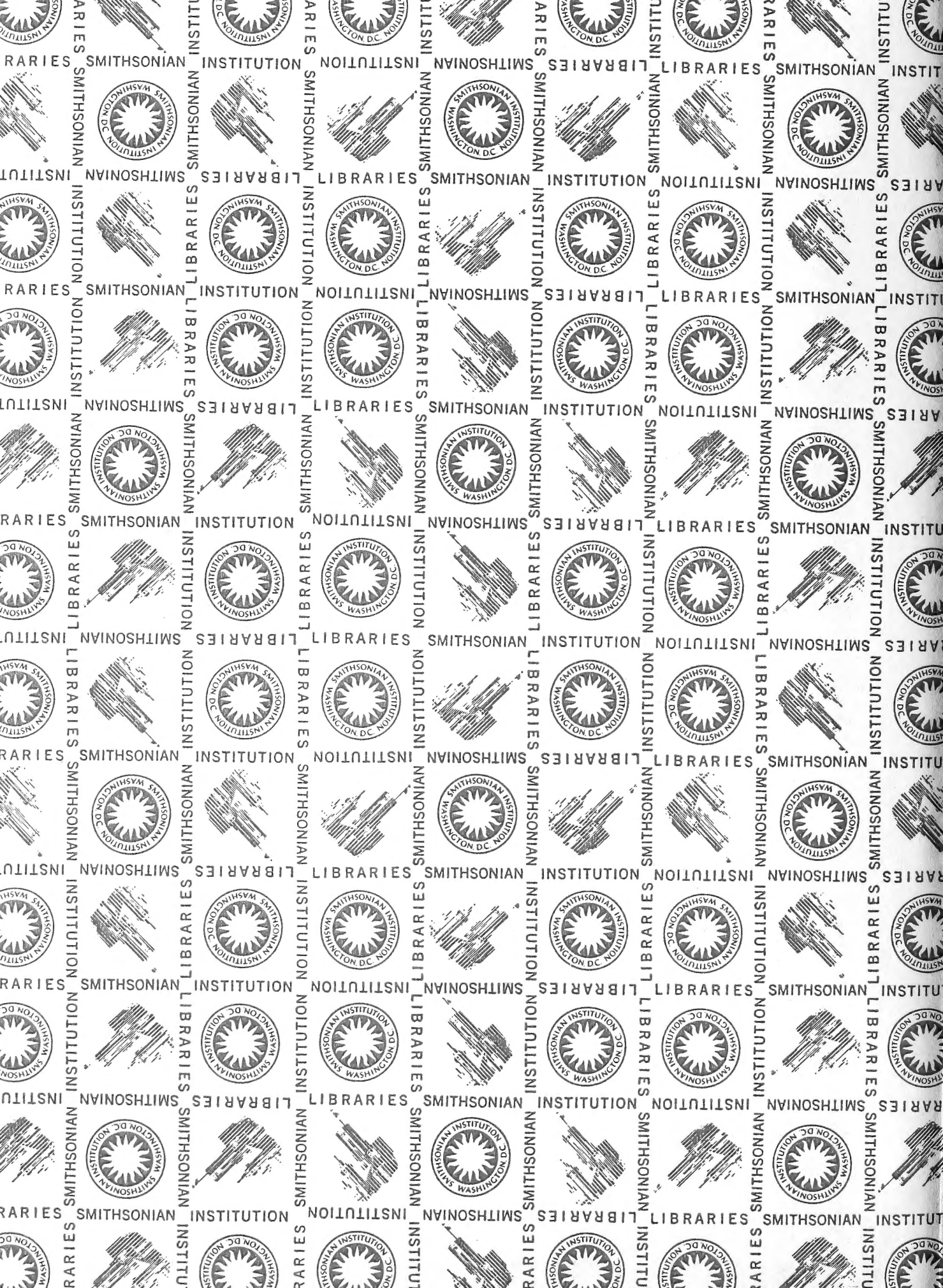
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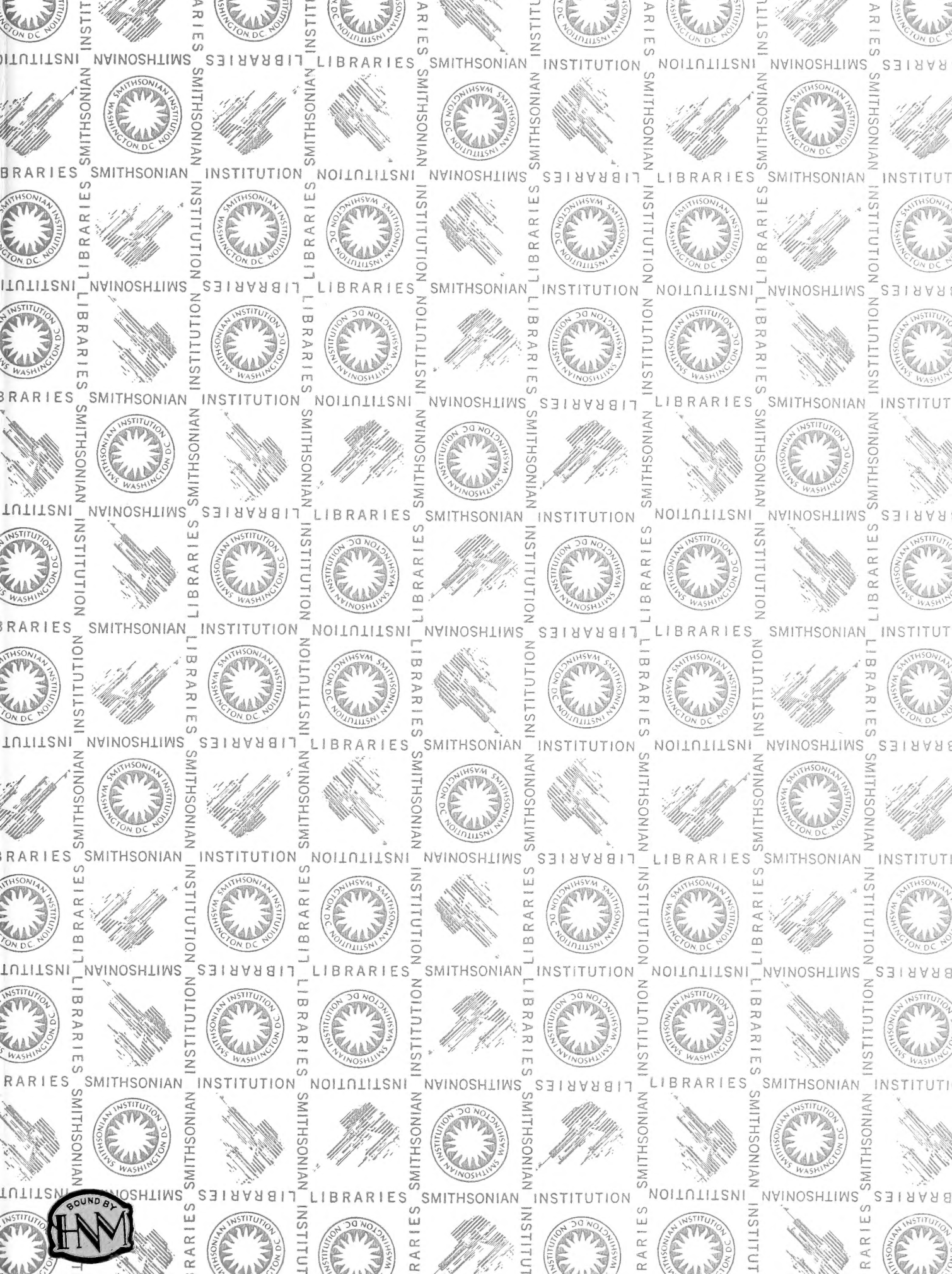
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